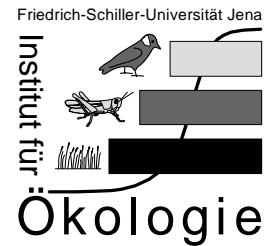




seit 1558



Nestling begging strategies in Wilson's storm- petrels (*Oceanites oceanicus*)

— Insights from a supplementary feeding experiment

Diplomarbeit

vorgelegt von

Anja Nordt

im September 2007

Institut für Ökologie

Biologisch-Pharmazeutische Fakultät

Friedrich-Schiller-Universität Jena

Betreuer: Prof. Dr. Stefan Halle, Jena

Dr. Hans-Ulrich Peter, Jena

Contents

1. Introduction	3
2. Methods	9
2.1. Study object	9
2.2. Study site and investigation period	10
2.3. Measurements	11
2.4. Sexing of chicks and adults	13
2.5. Estimation of meal size and manipulation by supplemental feeding	14
2.6. Records of feeding visits	16
2.7. Analysis of begging calls	16
2.8. Statistics	19
3. Results	20
3.1. Chick development	20
3.2. Chick begging behaviour	24
3.3. Between year variability in call parameters	26
3.4. Between sexes and individual differences	26
3.5. Influences of body condition	27
3.6. Differences between first and second feeding events	29
3.7. Influences of supplementation on chick body condition and call features	30
3.8. Parent – offspring interactions	33
3.9. Sex specificity in provisioning rules	36
4. Discussion	37
4.1. Chick development	37
4.2. Honest signalling of need	39
4.3. Does supplementation affect chick’s honesty?	42
4.4. Bias in parental care and responsiveness	46
4.5. Conclusion and prospects	47
5. Summary	49
6. Zusammenfassung	50
7. References	52
8. Appendix	62
Appendix A: Statistic values of the influence of supplementation on call parameter	62
Appendix B: List of abbreviations and terms	64
9. Acknowledgements	65
10. Selbständigkeitserklärung	66

1. Introduction

The conspicuous begging display of young birds and mammals has become a model for studies on the evolution of animal signals (reviewed by [Kilner & Johnstone 1997](#)). During begging, a frequently used term to describe solicitation behaviour by chicks ([Ryden & Bengtsson 1980](#); [Christe et al. 1996](#)), altricial nestlings expose brightly coloured gapes, flap their wings and call loudly to obtain food from parents. Given the proximity of adult and young during signalling, this apparently vigorous display seems unnecessary or even costly in terms of predator attraction ([Leech & Leonard 1997](#); [Dearborn 1999](#)). Exaggerated begging can be seen as an expression of conflict over the allocation of limited resources between parents and their offspring ([Godfray 1991](#)), particularly in the context of life history theory and parent – offspring conflict.

Reproduction is costly ([Williams 1966](#); [Stearns 1992](#); [Wernham & Bryant 1998](#)), not only in terms of an enhanced foraging effort (e.g. [Roskaft 1985](#); [Reid 1987](#); [Gustafsson & Sutherland 1988](#)), but also regarding proximate mechanisms like the impact on hormones and immune functions, metabolism or stress tolerance (reviewed in [Harshman & Zera 2006](#)). Life history theory assumes that parents must regulate the investment into each breeding attempt to maximize their lifetime reproductive success ([Stearns 1992](#)). Reduced parental survival due to excessive investment at one breeding attempt may greatly decrease lifetime reproductive success ([Pugesek & Diem 1990](#)). Therefore, in long-living species the trade-off between current parental effort and residual reproductive value will be biased towards the latter ([Hamer et al. 1998](#)). Especially in poor seasons, parents are expected to reduce the quality of their offspring or abandon a breeding attempt rather than compromise their survival and future opportunities to reproduce ([Martin 1987](#); [Saether et al. 1993](#); [Weimerskirch et al. 1995](#); [Wernham & Bryant 1998](#); [Takahashi et al. 1999b](#)). So the optimal amount of investment for a parent to supply will not equal the optimal amount for an offspring to receive. From this clash of interests the parent – offspring conflict arises ([Trivers 1974](#)). Hence seemingly exaggerated begging was suggested to be a result of selection on offspring to manipulate parents into providing more resources than they have been selected to give ([Godfray 1991](#); [1995a](#); [Wells 2003](#)).

On the other hand, honest signalling models assume that begging reliably conveys aspects of offspring need that parents cannot assess directly ([Leonard & Horn 2001a](#)). Since adults need to balance their investment of limited resources carefully between self-feeding and food provisioning to the offspring ([Ydenberg 1994](#)), the information about the needs of their nestling would give them useful clues to facilitate the appraisal of food

delivery (Haig 1990). Herein, the term *need* describes the increase in an offspring's personal fitness resulting from ingesting a certain amount of food (Godfray 1991; Royle et al. 2002). The more a chick can benefit from a feed, the needier it is (Villaseñor & Drummond 2007). In many cases, need is likely to be a function of two main factors: short- and long-term needs (Price et al. 1996; Iacovides & Evans 1998). A chronic undernourished offspring that is underweight for its age can be satiated, having been fed recently, just as a well-fed nestling can be hungry. The first has pronounced long-term needs, which Price et al. (1996) defined to be the total amount of food required to fledge, while the latter's short time needs, i.e. its hunger level, are marked (Villaseñor & Drummond 2007).

The distinction between short- and long-term needs raises the question which aspects of offspring condition might be advertised during begging and whether distinct begging parameters convey information about different aspects of the chick's state. As several authors pointed out, the intensity of solicitation behaviour of a nestling encodes not only its needs, but can also be influenced by its age (Leonard et al. 1997; Clark & Lee 1998; Jurisevic 1999; Macgregor & Cockburn 2002; Gladbach 2005) or gender (Price et al. 1996; Quillfeldt et al. 2007b). Most studies on parent – offspring interactions have been carried out in passeriform birds, where nest mates compete for food and care, respectively access to the feeding parent (Choi & Bakken 1990; Price & Ydenberg 1995; Ottosson et al. 1997; Parker et al. 2002; Neuenschwander et al. 2003). For example Price et al. (1996) reported for Yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) that begging calls of chicks varied with the intensity of sibling competition but were independently of need. Contrarily, Cotton et al. (1996) provided experimental evidence that begging in European starling (*Sturnus vulgaris*) nestlings is purely a function of individual need and not influenced by siblings. Compared to the scramble competition among nest mates, which has been demonstrated to intensify begging displays (Smith & Montgomerie 1991; Price 1996; Leonard & Horn 2001a), predator avoidance acts as an attenuating selection pressure on this behaviour (Platzen & Magrath 2004). Kilner & Johnstone (1997) concluded that parent – offspring interactions are rarely as simple as signalling models assume. Data on information content of chicks' solicitation behaviour or parental resource allocation should be interpreted with caution, because signal intensity might be determined by need as well as by the potentially confounding factor of sibling competition (Kilner & Johnstone 1997; Krebs 2001). Thus Royle et al. (2002) stated the degree of reliance to be strongly context dependent. Begging might be a true signal of need only when the potential for conflict is low and food is not a limiting factor.

Addressing this question of honesty to avian species with single-chick-clutches, some complications are excluded since signalling can be studied in the absence of sibling competition. Potential study taxa, rearing single chick broods, can be found among penguins, auks, cockatoos and raptors (Quillfeldt 2002b). But the only order where all species have obligate clutch sizes of one egg are the Procellariiformes, *inter alia* comprising albatrosses, petrels and shearwaters (Warham 1990; 1996).

Quillfeldt & Masello (2004) posed a key question in parent – offspring conflict, namely whether resource allocation is controlled primarily by parents or by their offspring, and how this interaction is mediated behaviourally. Despite the great diversity of procellariiform seabirds, all species investigated so far seem to use structurally similar begging calls, which have a submissive connotation (Bretagnolle 1996). Nevertheless, controversy still exists regarding the information content of begging and the mechanisms underlying parental feeding decisions, although there is increasing evidence that food availability, adult experience and body condition, and the duration of foraging trip length during chick rearing play a central role in the regulation process (Chaurand & Weimerskirch 1994; Lorentsen 1996; Weimerskirch et al. 1997a; Weimerskirch et al. 2000).

Procellariiformes as long-living seabirds, exhibit an extreme pattern of development in which chicks accumulate enormous quantities of fat reserves during the nestling period and subsequently lose most of it prior to fledging (Ricklefs et al. 1980; Hamer et al. 1998). Chicks are fed large meals at long intervals of up to several days, with pair partners feeding independently from each other (e.g. Warham et al. 1977; Ricklefs et al. 1985; Hamer & Hill 1993). This prevents foraging adults from obtaining reliable information about the chick's food requirements at the next visit to the nest, because the nutritional state of a chick at one feeding may convey little information about its needs at the end of the parent's succeeding foraging trip (Hamer & Hill 1994). Given short-term stochastic variation in foraging success, the average level of food delivery should be higher than required to sustain average growth rates (Ricklefs & Schew 1994). This was expected to cause a chronic overprovisioning of the chick resulting in the accumulation of large amounts of adipose tissue due to an intrinsic rhythm of adult provisioning behaviour rather than being able to respond directly to the short-term needs at the nest (Ricklefs et al. 1985; Ricklefs 1987; 1992; Hamer & Hill 1993; 1994). This trait has been attributed to the low rate and irregular pattern of food provisioning under the limited and unpredictable marine food resources (Ricklefs 1992; Hamer 1994; Ricklefs & Schew 1994). This hypothesis was strongly supported by the observation of Hamer et al. (1997) that in chicks of the Short-

tailed shearwater (*Puffinus tenuirostris*), a species where feeding occurs less frequently and provisioning rates are highly variable, accumulation of large lipid reserves was even more pronounced. In this group, therefore, provisioning rate was supposed not to be influenced by the chick, through solicitation, but may instead be determined solely by the adults' ability to obtain food. At individual level, this will reflect stochastic variation in foraging success, while consistent differences between chicks are likely to occur as a result of variation in adult quality and experience (Hamer 1994).

On the other hand, in the early 1980's Harris (1983) already reported that Atlantic puffin (*Fratercula arctica*) parents are able to perceive the nutritional status of their nestlings through the intensity of the begging display. Subsequently, several experimental studies investigated the regulation of food delivery by adults, but results are equivocal. Nestling age, nutritional demand, or both were found to regulate parental provisioning in some studies of seabirds (Johnson et al. 1994, Cook & Hamer 1997, Erikstad et al. 1997, Wernham & Bryant 1998 and Harding et al. 2002 for puffins; Weimerskirch et al. 1997b, 2000 and Phillips & Croxall 2003 for albatrosses; Weimerskirch et al. 1995, Bolton 1995a, 1995b, Takahashi et al. 1999b, Hamer et al. 1998 and 2006 for petrels and storm-petrels; and Bertram et al. 1996 for Rhinoceros auklets (*Cerorhinca monocarata*)) but not in others (Hudson 1979 for the Atlantic puffin; Ricklefs 1987, 1992, Hamer & Hill 1993, 1994, Saether et al. 1993, Bradley et al. 2000 and Granadeiro et al. 2000 for petrels and storm-petrels, Takahashi et al. 1999a for the Rhinoceros auklet). The inter- and even intraspecific differences in parental response to experimental manipulation of chick food demand explained Bolton (1995b) and Takahashi et al. (1999b) by the differences in foraging trip duration. Parents of Procellariiformes changed food provisioning in accordance to their chick's need when individual adults attended the nestsite at average intervals of less than two days, while species performing foraging trips of more than two days cannot or do not respond to the requirements at the nest. This was traced back to the fact that a shorter feeding interval may provide parents with more chances to evaluate and respond to the changing nutritional status of their chick (Bolton 1995b).

The average feeding interval of Wilson's storm-petrel, the model organism chosen for this study, ranges from 1.3 to 3.3 nights per individual parent, depending on krill abundance and season (Quillfeldt & Peter 2000; Büßer et al. 2004). Nevertheless, it was assumed that nestlings of this species advertise their needs during begging and parents adjust their feeding decisions accordingly (Quillfeldt 2002a; Gladbach 2005). The acoustic repertoire of chicks consists of two types of calls, namely rhythmic and long calls. The former describes series of similar elements rapidly repeated at regular intervals. Single

elements of the latter are more extended and gaps between the calls are less regular. They are exclusively uttered in the presence of an adult to solicit food and thus are referred to as begging calls (Quillfeldt 2002a).

The purpose of this study was to examine how information on nestling need is encoded in the structure of begging calls given by Wilson's storm-petrel nestlings and whether this information is appropriate to the chick's need. In the analyses of begging calls three different approaches were combined. First, to ensure comparability with earlier studies which are based mainly on countable call parameters like call number and call rate (e.g. Granadeiro et al. 2000; Quillfeldt & Masello 2004; Quillfeldt et al. 2004; Hamer et al. 2006), these 'classic' call parameters were included in the study. However, they describe the begging call session rather than individual begging call elements and the information is not given until the end of the whole begging session. Since different components of certain signals may encode specific information, a single begging call could contain all particulars required for parents to adjust their provisioning to the chick's current needs. Therefore, more recent investigations on call characteristics often use acoustic call features derived from spectrogram analysis to test their information content regarding chick body condition (e.g. Price & Ydenberg 1995; Sacchi et al. 2002; Gladbach 2005; Trager et al. 2006; Quillfeldt et al. 2007b). Analyzing the acoustic structure of single elements of begging calls of Wilson's storm-petrels, e.g. the frequency or duration of a call element, was the second approach in this study. It was tested whether day-to-day variation in these parameters reflect the day-to-day variation in chick body condition. To concentrate possibly marginal effects of highly correlated acoustic call parameters, a Principal Component Analysis was accomplished, representing the third approach.

The responsiveness of parents to the information provided by their nestling was further examined. In case adult Wilson's storm-petrels adjust the provisioning effort to their chick's needs, provisioning parameters should change in accordance with nestling body condition. Parents may respond either directly by regurgitating more or less food, or later by altering the feeding frequency.

To address these questions of chick's honesty and adult's responsiveness, and to verify empirical findings, a supplementary feeding experiment was conducted. Providing additional food by supplementation was expected to, at least partly, satiate the chick and reduce its short-term needs. Thus, begging intensity should decrease in the course of the experiment if different begging parameters reveal aspects of chick's requirements or need

for food in particular. Furthermore, reduced begging should lead to diminution of provisioning effort by parents.

Finally, several authors reported differences between males and females in responsiveness to chick's needs (e.g. [Weimerskirch & Lys 2000](#); [Quillfeldt et al. 2004](#); [Hamer et al. 2006](#)). In Wilson's storm-petrels, adults show only a marginal sexual size dimorphism ([Büßer 2003](#)) and no extra-pair paternity occurs ([Quillfeldt et al. 2001](#)). Hence, a sex bias in parental investment or differences in responsiveness seem unlikely in this seabird species. Nevertheless, parental provisioning was examined separately regarding the sex of the feeding adult.

The following predictions were tested:

- (1) Different components of long begging calls contain information about the nutritional state of the nestling and thus differ with chick's need.
- (2) Parents are able to perceive this information provided and base their feeding decision on it.
- (3) Supplementation results in a decrease of begging intensity and consequently in reduced parental investment.
- (4) No differences in provisioning arise between males and females. Both sexes show equal responsiveness to their chick's needs.

To my knowledge, this investigation is the first one combining the experimental manipulation of chick body condition by supplementary feeding with the analysis of sonographic call features.

2. Methods

2.1. Study object

The Wilson's storm-petrel is with a wingspan of 42 cm, the smallest breeding bird in the Antarctic, but one of the most abundant seabirds worldwide (Del Hoyo et al. 1992). Over one million breeding pairs nest circumpolar on ice-free coasts of the Antarctic and subantarctic islands (Beck & Brown 1972; Marchant & Higgins 1990). They approach the breeding colony only during the reproductive period. Like the sympatric breeding and slightly bigger Black-bellied storm-petrel (*Fregetta tropica*) they use crevices and natural cavities in scree slopes as nest burrows. In order to avoid diurnal predators like Skuas (*Catharacta* spp.) and gulls (e.g. *Larus dominicanus*) they attend the breeding colony only at night (Hahn & Quillfeldt 1998).

With the other members of the very diverse order of Tubenoses (Procellariiformes) Wilson's storm-petrel shares a uniform life-history strategy. They have an obligate clutch size of one egg and a large slow-growing chick. Pair partners are socially and genetically monogamous (Quillfeldt et al. 2001) and both sexes are equally involved in the intensive parental care, like incubating the egg for 38 to 48 days followed by chick-rearing which lasts for 55 days, on average (Warham 1996).

As soon as the chick is able to maintain its body temperature by itself (1-2 days after hatching) it is left alone in the nest burrow during daytime while the adults forage at sea (Roberts 1940, Warham 1990). They prey mainly on krill, e.g. *Euphausia superba*, amphipods and small myctophid fish (Croxall et al. 1988; Quillfeldt 2002c). Chicks are fed during nightly visits at the nest with partly digested food items, but primarily with a high energy stomach oil, consisting of free lipids, fat-soluble pigments and water (Warham et al. 1976; Warham 1977; Obst & Nagy 1993). The food is delivered from adult to chick by approximately 30 beak-to-beak regurgitations (own observation). Since feedings occur only at night, feeding events are discrete and the recent feeding history can easily be classified (Quillfeldt 2002a).

2.2. Study site and investigation period

The study was carried out on King George Island ($62^{\circ}14'S$, $58^{\circ}40'W$), which belongs to the South Shetlands, an island chain approximately 100 km north of the Antarctic Peninsula (Fig. 2.1.). The study site is situated around the extinct and intensely eroded volcanic vent Cerro Tres Hermanos on the ice free Potter Peninsula about one kilometre away from the Argentinean Base Jubany.

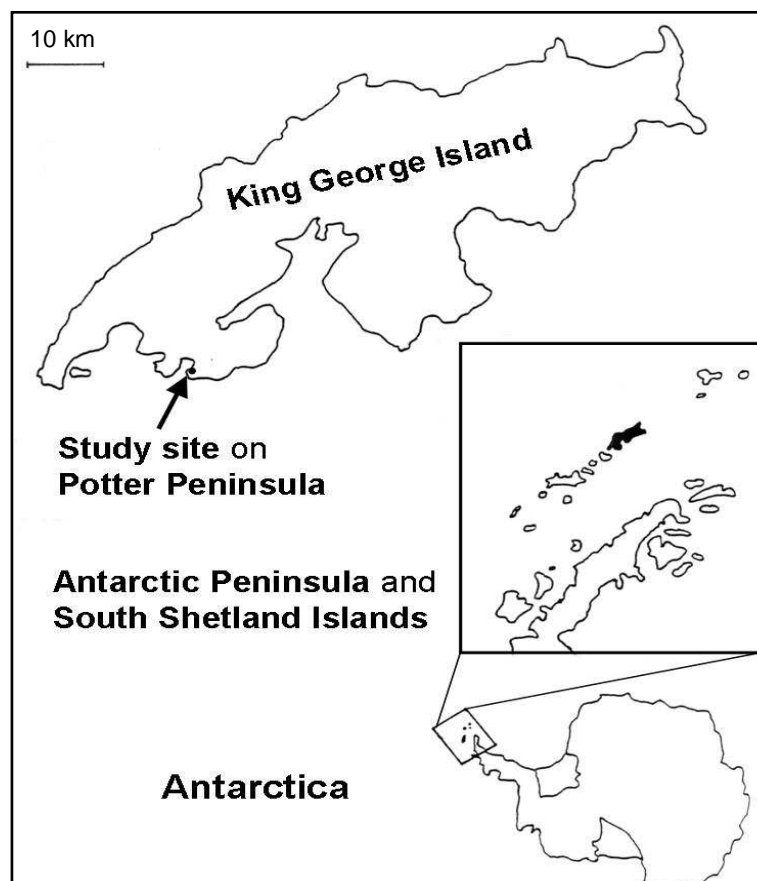


Fig. 2.1. Location of the study site on King George Island and its location to the Antarctic Peninsula.

Through degradation of the volcano the scree slopes consist of basalt boulders of 0.2 to 3 m in diameter. These rocks form natural cavities and in inactive areas, where slope failure and rock slide had come to an end, they are densely covered with different lichens, mainly from the genus *Usnea* (Hahn 1997). The cavities between and under the boulders are used by Wilson's storm-petrels for nesting. Since 1996 *O. oceanicus* has been monitored in this breeding colony. Its population size was estimated to 1400 to 2280 breeding pairs in 1996 (Hahn et al. 1998).

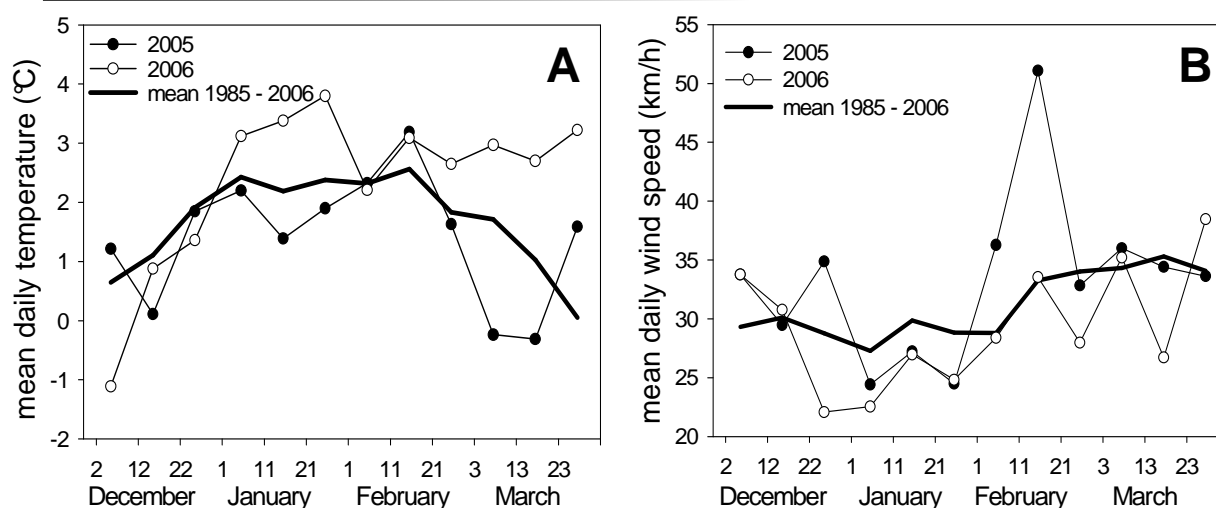


Fig. 2.2. Mean daily temperature (A) and mean daily wind speed (B) measured in the base Jubany in the seasons 2004/05 and 2005/06 compared to an average value covering 20 years (1985 – 2006). The means are stated per decade.

The weather of the study area is affected by its location in the westwind belt resulting in a maritime polar climate (Stonehouse 1989; Wunderle et al. 1998). It is characterized by moderate variations in temperature (Fig. 2.2., daily means ranging from -7°C to $+7^{\circ}\text{C}$ in summer months) and, for polar regions, relatively high precipitation (mean monthly rainfall over the last 20 years: 29.4 mm in December rising to 48.7 mm in March). Since the temperature can even in summer fall below the freezing point, occasionally snow storms are not unusual and can accumulate several decimetres of snow, posing a serious threat to the storm-petrels by blocking the nest entrances. Weather data were made available by the *Servicio Meteorológico Nacional* (Argentina).

The field work for this study was carried out in the Antarctic seasons of 2004/05 (December to March) and 2005/06 (January to March). In the following all year specifications refer to the second half of the austral summer, therefore ‘2005’ corresponds to the breeding season 2004/05.

2.3. Measurements

At the beginning of the season nests marked in previous years were checked for signs of activity like incubating adults or recently laid eggs. When an egg was detected, length and breadth were measured to the nearest 0.1 mm using a sliding calliper and it was weighed to the nearest 0.1 g using a digital balance. Adults inside the nest burrow were hand-captured, for monitoring purposes ringed and several morphometrics (length of head, beak and tarsus to the nearest 0.1 mm using a sliding calliper; length of tail, wing and eighth primary using

a stopped wing rule to the nearest millimetre) and the body weight (using the digital balance to the nearest 0.1 g) were measured. Furthermore, to differentiate between adults on the video tapes, one adult of each breeding pair of potential film nests was marked with a dot of white paint on the forehead and the bows of the wings. After handling the bird was replaced into its burrow to reduce the risk of being caught by an avian predator, notably Skuas.

Wilson's storm-petrels show a tendency to desert the nest after repeated disturbance during the incubation period (Beck & Brown 1972), hence the nests were not visited again until four days past the estimated hatching date. Since the egg loses water during incubation, its weight decreases up to 16% of the initial value (Rahn & Ar 1974). The hatching date can thus be calculated from egg density and volume according to following equation (Furness & Furness 1981; Quillfeldt & Peter 2000).

$$days_until_hatching = \frac{\left(\frac{mass}{length \cdot breadth^2 \cdot 0.507} \right) - 0.85 \frac{g}{cm^3}}{0.007 \frac{g}{cm^3}}$$

The absence of parents from the nest during the day a few days after their offspring has hatched provides the opportunity to handle the chick with relatively little disturbance to the adults. Chicks were weighed daily to the nearest 0.1 g using a digital balance respectively to the nearest 0.5 g using a Pesola spring balance in both late seasons due to failure of the digital balance. Weighing occurred every day in the same order and at approximately the same time for every chick. For further analysis the mass at a standardised time (14:00 h local time) was calculated taking into account the mass loss due to respiration and defecation (Quillfeldt & Peter 2000). Using these data the individual body condition of chicks was determined as the residual mass to the population mean mass of chicks of the same age and expressed as a proportion of the predicted values (Quillfeldt 2002a).

Procellariiform chicks have a typical growth curve of mass development with a period of rapid increase up to a peak followed by a period of slow decrease until fledging (Warham 1990). A good description of the period of mass increase up to peak mass provides the sigmoid Gompertz equation (Weimerskirch & Lys 2000; Bunce 2001) but it underestimates the peak mass if data of the pre-fledging mass recession are included. Therefore body mass development was characterized using the 'final curve' of Huin & Prince (2000) consisting of an original Gompertz curve and the production of a delayed inverse Gompertz curve:

$$mass = A \cdot e \left[-e^{-k_1(t-t_1)} - e^{k_2(t-t_2)} \right]$$

The chicks grow with the mass growth rate k_1 to an asymptotic mass A , having their fastest growth at the midpoint in mass $A/2$ at the time t_1 . After a period of relative stability, mass loss becomes more important with the maximum mass loss rate k_2 at the age t_2 . Due to the limited field season none of the chicks were observed to fledge and data of pre-fledging mass loss are not available for all chicks. In these cases the original Gompertz curve was used to determine the coefficients of individual body mass development.

To assess individual body growth rates, chicks were measured every third day after reaching a tarsus length of 20 mm, which occurs at an age of approximately 15 days. The length of tarsus, wing and if possible eighth primary and tail were determined as described above for adults. Individual growth rates for tarsus (k_t), wing (k_w), eighth primary (k_{tp}) and corresponding asymptotes (A) were evaluated by fitting following logistic growth curve to the data.

$$y = \frac{A}{1 + e^{-k(t-t_i)}}$$

In the equation t_i represents the time of inflection of the growth curve, respectively the time of maximum growth rate.

2.4. Sexing of chicks and adults

To determine the gender, blood samples were taken from adults during handling and from all chicks surviving until the end of the breeding season and being in a physical constitution where this interference was scientifically reasonable. Though avian erythrocytes still enclose the cell nucleus, very little whole blood contains sufficient DNA for the method of DNA-sexing. Female birds are heterogametic (ZW) while males are homogametic (ZZ), thus the sex of a bird of unknown gender can be determined by detecting the presence of a W chromosome sequence (females) or its absence (males; [Fridolfsson & Ellegren 1999](#)).

Blood samples were taken by puncturing the ulnar vein (*Vena ulnaris*) with a sterile canula. The leaking drop of blood (about 50 μ l) was transferred via heparinized capillaries to 500 μ l APS buffer ([Arctander 1988](#)). To stanch the bleeding, cellulose was pressed upon the lesion. The samples were stored at -20°C until further processing.

DNA was isolated from blood cells and precipitated with ethyl alcohol according to a standard procedure ([Miller et al. 1988](#)) modified by [Lubjuhn & Sauer \(1999\)](#). The method described in [Fridolfsson & Ellegren \(1999\)](#) was used to differentiate between the sexes, since females are characterized by displaying two fragments after PCR amplifikation with



Fig. 2.3. Pattern of DNA-bands after separating the DNA fragments by gel electrophoresis and visualizing by ethidium bromide staining. Samples with two bands (e.g. samples 1 and 2 on the left) are determined as females, one band indicating males (e.g. samples 3 and 4).

specific primers and the separation in a gel electrophoresis, while males only show one DNA band (Fig. 2.3.).

2.5. Estimation of meal sizes and manipulation by supplemental feeding

Meal sizes were calculated by correcting the difference between daily weightings for metabolic mass loss (Ricklefs et al. 1985; Quillfeldt & Peter 2000). Due to functional limits of the adult's capacity of carrying food, calculated meal sizes up to 13 g were defined as single feeding, while meal sizes exceeding 13 g were defined to represent two feeding events assuming both parents to contribute equally to the detected total meal size (Obst & Nagy 1993; Quillfeldt & Peter 2000). If feeding events of two adults were directly observed on the videotape, two feeding events were registered, even if the total meal size was less than 13 g. The total meal size was then partitioned according to the observed number of food regurgitations per parent (Büßer 2003).

Unfed chicks with an observed mass change higher than the estimated metabolic mass loss indicate that a certain number of chicks lose more than the average weight over the day. This number was assumed to reflect the same number of chicks, which lose less than the average amount of mass. An equivalent number of chicks were therefore stated as 'unfed' despite of a computed small meal intake.

In very young chicks meal size is not independent from chick age (Quillfeldt & Peter 2000), but is constrained by the ability of the chick to swallow a certain amount of food. To exclude this influence, only calculated meal sizes of chicks older than 10 days were included in the analysis.

During the treatment period, chicks were given supplemental food consisting of cod liver oil (Pure Cod Liver Oil by Superdrug Stores PLC, Croydon/UK) to manipulate their

hunger level. The energy content of the oil of 39.7 kJ/g (Heseker & Heseker 1993) is quite similar to the value for stomach oil of Procellariiformes (40 kJ/g, Warham et al. 1976). The amount of food supplemented to chicks was calculated so as to induce some improvement in body condition without overburdening their digestive capacity, which could affect the ability to accept more food from their parents. The provided supplement was calculated to constitute 50 % of the daily energy requirement of the chick of a defined age based on the energy values given in Obst & Nagy (1993) and assuming an assimilation efficiency of 90 % (Bolton 1995a). So calculated doses of supplement ranged between 1.6 g and 2.8 g (Fig. 2.4.) representing 14-33 % of the mean nightly food delivery by the parents (Quillfeldt & Peter 2000).

Each meal has been hand-warmed before introduction. The cod liver oil was directly introduced to the chick's esophagus by a small flexible tube using a 10 ml syringe. None of the chicks receiving the supplement regurgitated any food. Small amounts of unswallowed oil were negligible.

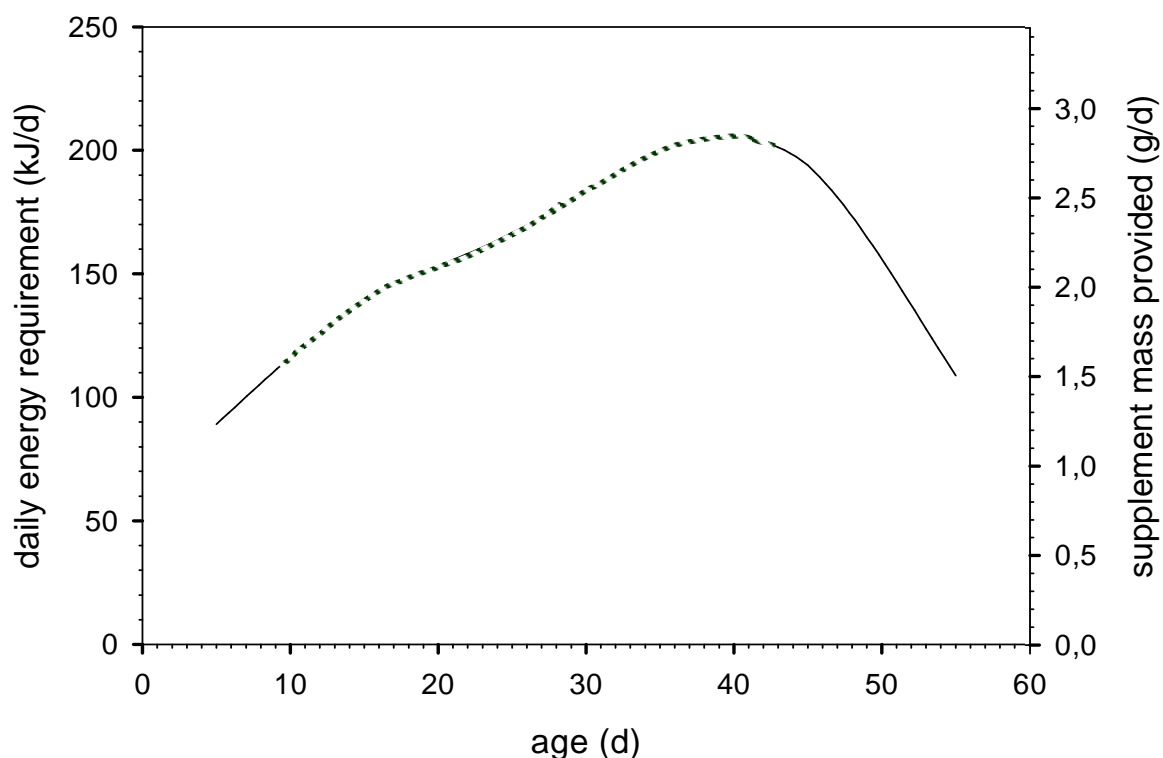


Fig. 2.4. Daily energy requirements for metabolism and tissue growth of Wilson's storm-petrel nestlings in dependence of age (left scale) and the thereafter calculated mass of artificial food supply (right scale). The dotted line marks the range of age classes where supplementation took place.

2.6. Records of feeding visits

The nightly behaviour of nestlings and provisioning adults was recorded using an infrared camera system (described in [Masello et al. 2001](#)). This installation consisted of a miniature camera with infra-red illumination and a built-in microphone, connected to a video cassette recorder (Toshiba V-210EG). Power supply was ensured by two charge-coupled 12 V SLA batteries which were protected against cold and wetness. The camera was placed inside the nest burrow approximately 10-20 cm from the chick. Every night before sunset, the system was provided with recharged batteries, an empty video tape and started in the longplay mode to cover a recording time of up to eight hours continuously. To detect relatively rare feeding events during daytime, filmed chicks were weighed again prior to starting the record.

Due to a high between chick variability regarding the begging parameters ([Quillfeldt 2002a](#)) each chick served as its own control. Therefore two nights per chick were first recorded without manipulation, referred to as control period. In the subsequent two nights, the treatment period, the chick received food supplementation directly before starting the record.

The tapes provided the basis for the analysis of acoustic parameters of nestling begging display and furthermore, chick provisioning could be quantified, e.g. feeding frequency, time of arrival and identity of the provisioning adult (presence of leg rings or plumage markers), beginning and duration of feedings and number of food transfers during one feeding event.

2.7. Analysis of begging calls

A begging session was defined to start with the first long begging call uttered due to an arriving adult and to end with the last begging call, followed only by rhythmic call series or silence, independent of continuation or termination of feeding. For the analysis of the vocal behaviour of nestlings during feeding events, audio streams from the video records were digitized at a sample rate of 16 kHz and 16 bit resolution using Cool Edit Pro 2.0. For all recorded begging sessions (58 in 2005 and 46 in 2006), the following classic call parameters were measured by counting from the digitized records or directly from the video tapes: the duration of the begging session (in min), the total number of begging calls per session, the call rate over the complete session (begging calls per min) and the

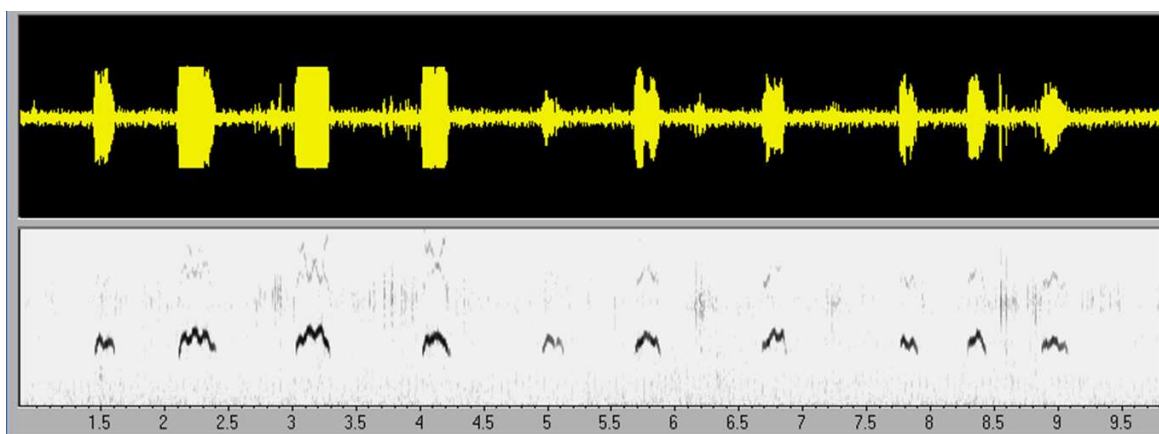
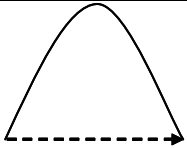
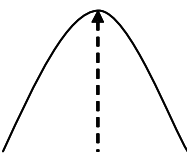


Fig. 2.5. Envelope curve (top) and spectral view (bottom) of ten calls of a begging session in AviSoft 4.2.

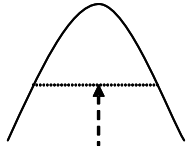
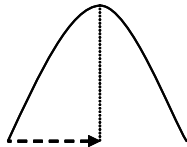

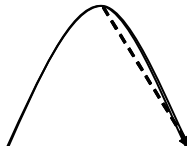
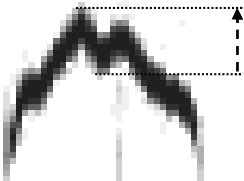
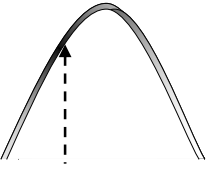
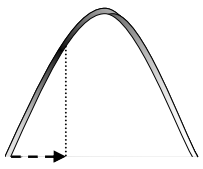
maximum call rate sustained for one minute (begging calls per min).

Furthermore, from each feeding session 15-20 individual calls were selected for the analysis of acoustic parameters. The difference in number is due to very low call rate in some cases. The calls were taken from the beginning of the begging session but recording quality was taken into account (good signal quality and absence of interfering calls from attending adults or neighbours). From these calls spectrograms were calculated using AviSoft 4.2 (FFT-length: 512, time resolution: 1 ms, frequency range: 0-8 kHz, Fig. 2.5.). The spectrograms were required for the semi-automatic analysis of acoustic call parameters using the software ConAn 0.93 (by R. Mundry, described in [Mundy & Sommer 2004](#)). From the output of ConAn 0.93 eleven parameters were chosen for the statistical analysis of the begging calls. They included the duration of a single call element, four frequency parameters and six describing the acoustic structure of a call (for further explanation see Tab. 2.1.).

Tab. 2.1. Sonographic call parameters determined in ConAn 0.93. Modified after [Glabach \(2005\)](#).

Abbreviation	Call Feature	Unit	Illustration
Duration	Duration of syllable	ms	
FMax	Maximum frequency of the element	Hz	

Tab. 2.1. (continued) Sonographic call parameters determined in ConAn 0.93. Modified after Gladbach (2005).

Abbreviation	Call Feature	Unit	Illustration
FMean	Mean frequency of the element	Hz	
LocFMax	Relative location of FMax normalised to element's duration	-	
LFMaxAbs	Absolute location of FMax from beginning of the element	ms	
SISStMax	Difference in frequency from start to FMax divided by LFMaxAbs	$\frac{Hz}{ms}$	
SIMaxEnd	Difference in frequency from FMax to element's end divided by duration LFMaxAbs to end	$\frac{Hz}{ms}$	
BroadTot	Frequency breadth of the element	Hz	
PeakFTot	Frequency at which the maximum energy is concentrated (rather frequency with largest amplitude)	Hz	
LMaxAmp	Relative location of maximum amplitude normalised to elements duration	-	
LMA_Abs	Absolute location of maximum amplitude from beginning of the element	ms	

A further interesting factor would have been the maximum amplitude, thus the volume of begging calls, but it was excluded from analysis since it is not independent from the distance between microphone and chick, which could not be ensured to be standardized for all records. Data for all call features were measured separately for each of the 15-20 calls of a begging session and afterwards averaged to obtain a mean value for the whole begging session.

Scarce recording quality due to heavy background noise caused by wind excluded eight records from processing in ConAn 0.93 which reduced the sample size to 50 in 2005.

In the analysis of the effect of body condition on call features only first feeding events per night per individual chick (i.e. chick-night) were included. Daily variation in the begging behaviour is therefore supposed to reflect the chick's need at the time of adult arrival. The first recorded begging session per chick-night was further used to test whether the classic call parameters were correlated to each other.

Sixteen (in 2005) and eight (in 2006) second feeding events were recorded and tested for differences in call parameters expecting that the second begging session per night is influenced by satiation.

2.8. Statistics

Statistical tests were performed using SigmaStat 2.03 and SPSS (versions 11.0 and 13.0). Figures were created in SigmaPlot 8.0 and SPSS. All tests were two-tailed and values are given as mean \pm standard error, except where stated otherwise.

A t-test was conducted to control for differences in chick body condition in both years in order to combine the two datasets in case the variations are independent from year. Where it revealed an influence of season, all analyses were repeated for both years separately.

To test for the influences of chick body condition and supplementation treatment on calling and from calling on chick provisioning, General Linear Models (GLM) and associated posthoc-tests were used. In order to control for individual differences between chicks, *nest* was included as categorical independent variable ('fixed factor'). Initially, interactions between covariates were included as further covariates, but removed as it did not reveal significance ($P > 0.25$).

Furthermore, highly correlated call variables were combined in factors using a Principal Component Analysis (PCA). This approach is a technique used to reduce multidimensional data sets to lower dimensions for analysis by retaining those characteristics of the data set that contribute most to its variance.

3. Results

3.1. Chick development

3.1.1. Chick growth

Throughout the fledging period, changes in the individual mass of chicks showed repeated periods of decrease, corresponding to the assimilation of food, with steep increase after receiving meal.

Chick body mass development in Wilson's storm-petrels combined for all chicks of 2005 (n=91) and 2006 (n=90) respectively, showed the typical pattern of procellariiform seabirds (Fig. 3.1.). The curves were best described by the following equations.

For 2005: $mass = 66.63 \cdot e^{-e^{-0.09 \cdot (age-8.55)}} - e^{0.03 \cdot (age-74.38)}$
 $R^2 = 0.65,$ $df = 2011,$ $F = 933.84,$ $P < 0.001$

For 2006: $mass = 63.49 \cdot e^{-e^{-0.09 \cdot (age-8.29)}} - e^{0.03 \cdot (age-116.96)}$
 $R^2 = 0.76,$ $df = 2658,$ $F = 2143.74,$ $P < 0.001$

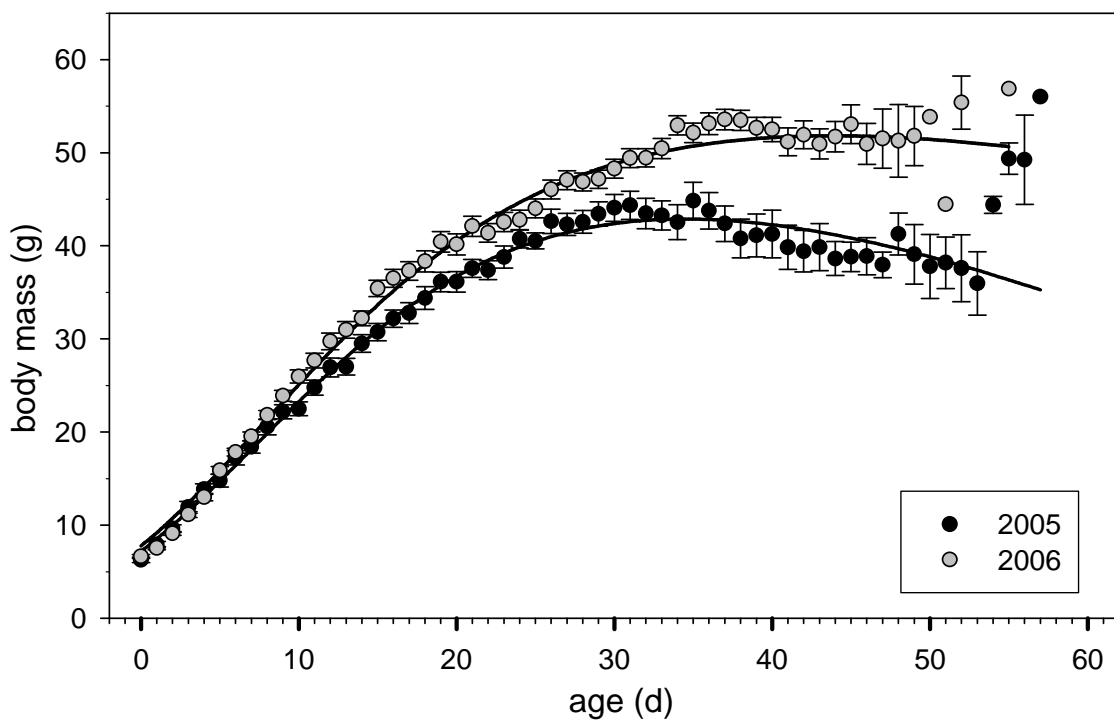


Fig. 3.1. Body mass growth curves for Wilson's storm-petrel chicks in the field seasons 2005 (filled circles) and 2006 (grey circles). The steep increase of values of the last four age classes in 2005 is based on two heavy chicks.

Coefficients of body mass development computed from individual growth curves, differed significantly between the two seasons (ANOVA for peak mass: $F_{135} = 17.87$, $p < 0.001$; age at peak mass: $F_{70} = 12.48$, $p = 0.001$; growth rate: $F_{135} = 4.20$, $p = 0.042$). In 2005 the peak mass of 43.97 ± 1.16 g was reached at an age of 26.19 ± 1.04 days, while in 2006 nestlings needed 31.91 ± 1.25 days to achieve their maximum weight of 62.15 ± 3.84 g. The mean growth rate of body mass in the first season exceeded the one of 2006 with 0.14 ± 0.01 to 0.12 ± 0.01 . The GLM revealed further an influence of the hatching date on growth rate ($F_{135} = 7.84$, $p = 0.006$) and age at peak mass ($F_{70} = 19.31$,

Tab. 3.1. Effects of year, hatching date, treatment and gender of chick on different growth parameters. (ANOVA, significant *P*-values are marked bold).

Source	d.f.	F	P
tarsus growth rate			
year	1	3.374	0.071
hatching date	1	2.698	0.106
treatment	1	1.456	0.232
sex	1	0.885	0.350
total	70		
tarsus length asymptote			
year	1	3.809	0.055
hatching date	1	25.332	< 0.001
treatment	1	0.332	0.572
sex	1	1.079	0.303
total	70		
wing growth rate			
year	1	26.978	< 0.001
hatching date	1	45.547	< 0.001
treatment	1	0.081	0.777
sex	1	0.344	0.559
total	98		
wing length asymptote			
year	1	7.395	0.008
hatching date	1	2.378	0.126
treatment	1	0.314	0.576
sex	1	1.605	0.208
total	98		
eighth primary growth rate			
year	1	56.367	< 0.001
hatching date	1	75.434	< 0.001
treatment	1	0.808	0.371
sex	1	0.103	0.749
total	97		
eighth primary length asymptote			
year	1	0.193	0.661
hatching date	1	0.491	0.485
treatment	1	0.002	0.967
sex	1	1.173	0.282
total	97		

$p < 0.001$) with later hatched chicks growing faster and reaching the peak mass at an earlier age. There was no detectable difference in any growth parameter between the sexes or treatment and control group.

The ANOVA of effects on different body growth parameters gave conforming results (Tab. 3.1.). In 2006 hatched chicks showed slower growth of wing and eighth primary, but their wings became larger (wing length asymptote in 2005: 14.62 ± 3.17 cm, respectively 15.32 ± 0.63 cm in 2006). Differences in tarsus growth between the two seasons were not significant but showed a similar tendency just as wing and eighth primary growth. Growth rates of wing and primary were further subject to influence of chick's hatching date. Later hatched chicks reached a higher maximum growth rate to obtain comparable ultimate values. Only the asymptote of tarsus length differed between early and late nestlings by being larger in later hatched chicks (Pearson Correlation Index of 0.046, $p < 0.001$). According to the body mass development, the experimental treatment and the chick's sex had no effect on body growth parameters.

3.1.2. Nestling body condition

The body condition of all nestlings older than four days ranged between -0.65 and 1.97. This value strongly differed between individual chicks (ANOVA for nest: $F_{27} = 7.96$, $p < 0.001$) and was significantly influenced by the feeding history (number of feds in previous night: $F_{74} = 33.70$, $p < 0.001$). Recently fed nestlings exhibited a higher level of nutritional state. The chicks age ($F_{74} = 0.006$, $p = 0.939$) or gender ($F_{55} = 0.329$, $p = 0.568$) had no influence on its body condition.

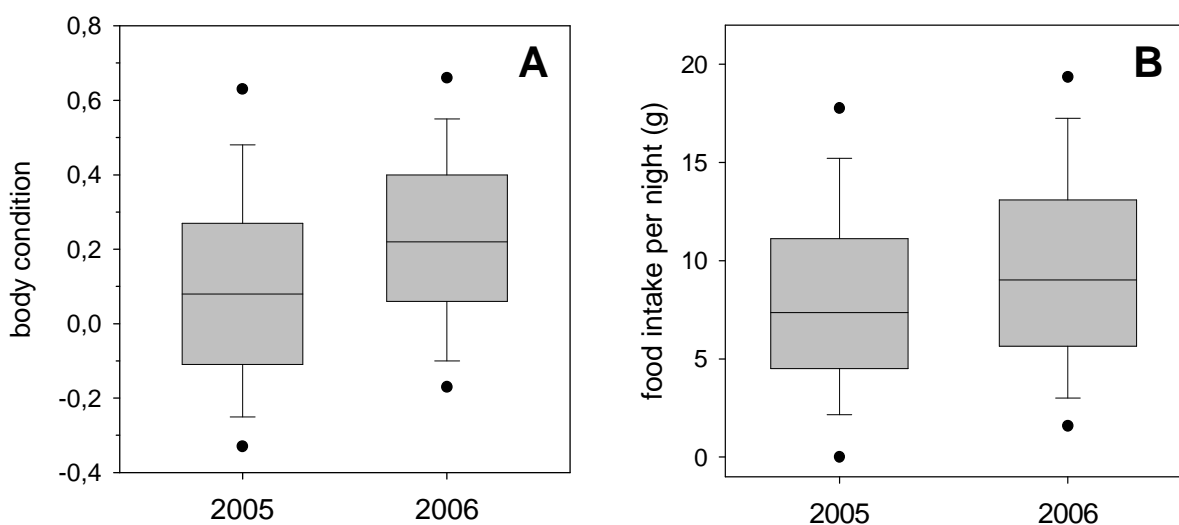


Fig. 3.2. Differences between the two seasons in nestling body condition (A) and amount of food received per night from parents (B).

The mean body condition of the season was 2006 with 0.236 ± 0.005 ($n = 2523$) significantly higher than in 2005 (0.107 ± 0.007 , $n = 1909$; Mann-Whitney U Test, $p < 0.001$; Fig. 3.2.A). Since body condition is determined from individual body mass related to the age class mean, these findings reflected the food amount provided by the parents per night (Fig. 3.2.B). In 2005 chicks received 8.11 ± 0.11 g of food during a night while parents provided their nestlings in the second season 9.60 ± 0.12 g per night, on average. This difference was highly significant (Mann-Whitney U Test, $p < 0.001$) and is mainly caused by a higher feeding frequency in 2006 (1.24 ± 0.01 feeding visits per night compared to 1.12 ± 0.01 in 2005, $t = -5.010$, $p < 0.001$, $df = 4194$), whereas the slightly larger amount of food provided per feeding event (2005: 7.33 ± 0.74 g; 2006: 7.45 ± 0.57 g) was only marginal (Mann-Whitney U Test, $p = 0.052$). Thus in 2006 adults came more often to the nest to feed their chick, but carried a similar amount of food compared to the poorer season of 2005.

3.1.3. Breeding success

The overall breeding success differed considerable between the two seasons investigated in this study (z – test: $z = 9.923$, $p < 0.001$; Tab. 3.2.). In 2005 the chick survival was very low due to severe snow storms during the chick rearing period. Comparable adverse weather conditions occurred in 2006 less often and due to the fact that chicks were in a good nutritional state most of them survived these hunger periods.

The proportion of fledged chicks among experimental nests was slightly enhanced compared to all nests (2005: 27.8 % versus 13.2 %; 2006: 100 % versus 84.8 %). This possibly indicates a positive effect of the additional food supply. However, these differences were not significant (z – test, 2005: $z = 1.205$, $p = 0.228$; 2006: $z = 0.991$, $p = 0.322$).

Tab. 3.2. Breeding success and mean date of hatching in the two observed seasons.

Season	2005	2006
No. of nests with egg	211	165
No. of eggs hatched	111 (52.61 %)	107 (64.85 %)
Mean date of hatching	6 th February	12 th February
No. of chicks fledged	17	79
Fledging success of chicks	15.32 %	73.83 %
Fledging success of eggs	8.07 %	47.88 %

3.2. Chick begging behaviour

3.2.1. Classic call parameter

In response to the arrival of an adult, Wilson's storm-petrel chicks started to utter some series of rhythmic calls, followed by long begging calls used exclusively during feeding. Begging sessions took 7.93 ± 0.49 min to complete (range 2 – 20 min). The number of long calls per session averaged 196.8 ± 15.91 (range 11 – 613 calls). The mean call rate was 23.31 ± 1.33 calls per min (range 2.93 – 50.58 calls/min), while the maximum call rate sustained for one minute averaged 39.96 ± 1.68 calls per min (range 7 – 63 calls/min).

In first begging session per chick-night all classic call parameters were significant correlated to each other except the combination of session duration and call rate (Tab. 3.3.).

Tab. 3.3. Pairwise correlations between the four classic call parameters. Only first feedings were included. (Pearson Correlation, significant *P*– values are marked bold).

	Call rate	Maximum call rate	Duration begging session
Number of long calls			
Correlation Coefficient	0.690	0.701	0.720
P	< 0.001	< 0.001	< 0.001
N	77	77	77
Call rate			
Correlation Coefficient		0.808	0.179
P		< 0.001	0.119
N		77	77
Maximum call rate			
Correlation Coefficient			0.389
P			< 0.001
N			77

3.2.2. Sonographic call features

A typical long begging call lasted 29.61 ± 0.75 ms, ranging from 16.90 to 51.60 ms, and had a mean frequency (FMean) between 2479 and 6591 Hz (mean 4008 ± 98.3 Hz). The maximum frequency (FMax) of 4997 ± 103.6 Hz on average, ranged from 3246 to 7720 Hz and was reached 13.17 ± 0.44 ms (LFMaxAbs, range 4.85 to 26.90 ms) after the beginning of the element, or relative to its duration (LocFMax) at 0.446 ± 0.009 , respectively, ranging from 0.240 to 0.651. SIStMax, which represented the slope of the

frequency from beginning of the element to its maximum, varied from 42.7 to 1308 Hz / ms and averaged at 258.8 ± 24.9 Hz / ms. The frequency descent from maximum to the element's end (SI_{MaxEnd}) was less steeply with -194.0 ± 20.8 Hz / ms, ranging from -1506 to -23.1 Hz / ms. The maximum amplitude was reached 13.97 ± 0.45 ms after the element's start (LMA_Abs, range 5.47 to 30.28 ms), respectively at 0.48 ± 0.01 relative to the element's duration (LMaxAmp), ranging from 0.12 to 0.86. The frequency with the largest amplitude (PeakFTot) varied between 2080 and 7320 Hz (mean 4232 ± 114 Hz). The mean breadth of elements (BroadTot) covered 1826 ± 80.0 Hz, ranging from 748 to 3629 Hz.

3.2.3. Principal Component Analysis

The Principal Component Analysis extracted four factors with Eigenvalues in excess of one, together explaining 84.7 % of the total variance (Tab. 3.4.). The first factor was mainly correlated with the frequency parameters FMean, FMax and PeakFTot. The second as well as the third factor described the acoustic structure of elements regarding the course of frequency (SI_{MaxEnd}, SI_{StMax}, BroadTot, Duration), respectively the location of the peak frequency (LF_{MaxAbs}, LocFMax). The two parameters of peak amplitude location (LMA_Abs, LMaxAmp) were combined with the element's duration in factor four.

Tab. 3.4. Eigenvalues, explained variance and rotated component matrix of factors extracted by a PCA of sonographic call features of long begging calls. Used rotation method was varimax with Kaiser normalization. Absolute coefficients in excess of 0.5 are marked bold.

	PCA factor			
	1	2	3	4
Initial Eigenvalues	4.2	2.3	1.7	1.2
Variance explained by factor in %	37.90	20.50	15.27	11.00
FMean	0.982	0.119	-0.026	0.062
PeakFTot	0.972	0.114	0.039	0.104
FMax	0.901	0.311	-0.080	0.113
SI _{MaxEnd}	-0.166	-0.792	-0.213	0.182
BroadTot	0.169	0.782	0.013	0.121
SI _{StMax}	0.110	0.718	-0.337	0.035
Duration	-0.322	-0.519	0.411	0.514
LF _{MaxAbs}	-0.170	-0.289	0.879	0.266
LocFMax	0.125	0.198	0.875	-0.203
LMA_Abs	0.126	-0.106	0.073	0.969
LMaxAmp	0.392	0.363	-0.229	0.686

3.3. Between year variability in call parameters

The season did not have a recognizable effect on any of the four parameters based on call counts (t-test for number of long calls: $t_{102} = 0.874$, $p = 0.384$; call rate: $t_{103} = -0.107$, $p = 0.915$; maximum call rate: $t_{103} = 0.072$, $p = 0.943$; duration of the begging session: $t_{102} = 0.721$, $p = 0.472$).

In contrast all acoustic call features, except LocFMax and LMA_Abs, significantly differed between the two seasons. Frequency parameters decreased from 2005 to 2006 (FMax: $t_{94} = 11.59$, $p < 0.001$; FMean: $t_{94} = 1.575$, $p < 0.001$; PeakFTot: $t_{94} = 10.60$, $p < 0.001$; BroadTot: $t_{94} = 5.155$, $p < 0.001$), while LMaxAbs increased ($t_{94} = -3.309$, $p = 0.001$) indicating that the location of peak frequency was shifted towards the end of the element in the second season. The mean call duration was higher in 2006 ($t_{94} = -6.652$, $p < 0.001$) and the calls flattened since SIStMax decreased ($t_{94} = 4.280$, $p < 0.001$) and SIMaxEnd increased ($t_{94} = -4.973$, $p < 0.001$), i.e. was less negative. The peak amplitude was reached sooner in 2006 (LMaxAmp: $t_{94} = 3.650$, $p < 0.001$).

Consistent results were obtained for the corresponding PCA factors. Factor 1 had a significantly lower mean value in 2006 ($t_{94} = 10.27$, $p < 0.001$) and factor 2 increased in the same time ($t_{94} = 4.693$, $p < 0.001$). The remaining factors 3 and 4 did not change between the years.

3.4. Between sexes and individual differences

3.4.1. Gender specific and individual differences in classic call parameters

For the number of long calls uttered during a feeding session (ANOVA, $F_{73} = 1.951$, $p = 0.167$), the overall call rate ($F_{74} = 0.667$, $p = 0.417$) and the duration of the begging session ($F_{73} = 0.303$, $p = 0.584$) were no differences found between the sexes. Only the maximum call rate differed significantly ($F_{74} = 5.40$, $p = 0.023$), with males calling at a higher rate than female nestlings.

The between-chick variability was very high for all four classic call parameters (ANOVA for call number: $F_{27} = 3.87$, $p < 0.001$; call rate: $F_{27} = 5.54$, $p < 0.001$; maximum call rate: $F_{27} = 6.05$, $p < 0.001$; duration of begging session: $F_{27} = 2.72$, $p = 0.001$).

3.4.2. Gender specific and individual differences in sonographic call features

Two out of the eleven acoustic call features depended on the chick's sex. Males reached the maximum amplitude of a call element significantly earlier than females (ANOVA for LMaxAmp: $F_{66} = 7.03$, $p = 0.010$; LMA_Abs: $F_{66} = 13.13$, $p = 0.001$). All other sonographic parameters showed no between sex variation.

Chicks of both sexes differed significantly in all frequency parameters (ANOVA for FMax: $F_{27} = 21.41$, $p < 0.001$; FMean: $F_{27} = 18.85$, $p < 0.001$; PeakFTot: $F_{27} = 14.70$, $p < 0.001$; BroadTot: $F_{27} = 4.22$, $p < 0.001$). The duration of an element, the slope to the frequency maximum and from maximum to the end showed significant variation between chicks, too (ANOVA for duration: $F_{27} = 6.50$, $p < 0.001$; SIStMax: $F_{27} = 1.76$, $p = 0.03$; SIMaxEnd: $F_{27} = 7.61$, $p < 0.001$). Individual differences were also found in the location parameters, e.g. in relative and absolute location of the maximum amplitude (LMaxAmp: $F_{27} = 4.05$, $p < 0.001$; LMA_Abs: $F_{27} = 3.27$, $p < 0.001$) and in the absolute location of the peak frequency (LFMaxAbs: $F_{27} = 2.55$, $p = 0.001$). Only the relative location of maximum frequency did not differ between the chicks (LocFMax: $F_{27} = 1.31$, $p = 0.18$).

3.4.3. Gender specificity and individuality in PCA factors

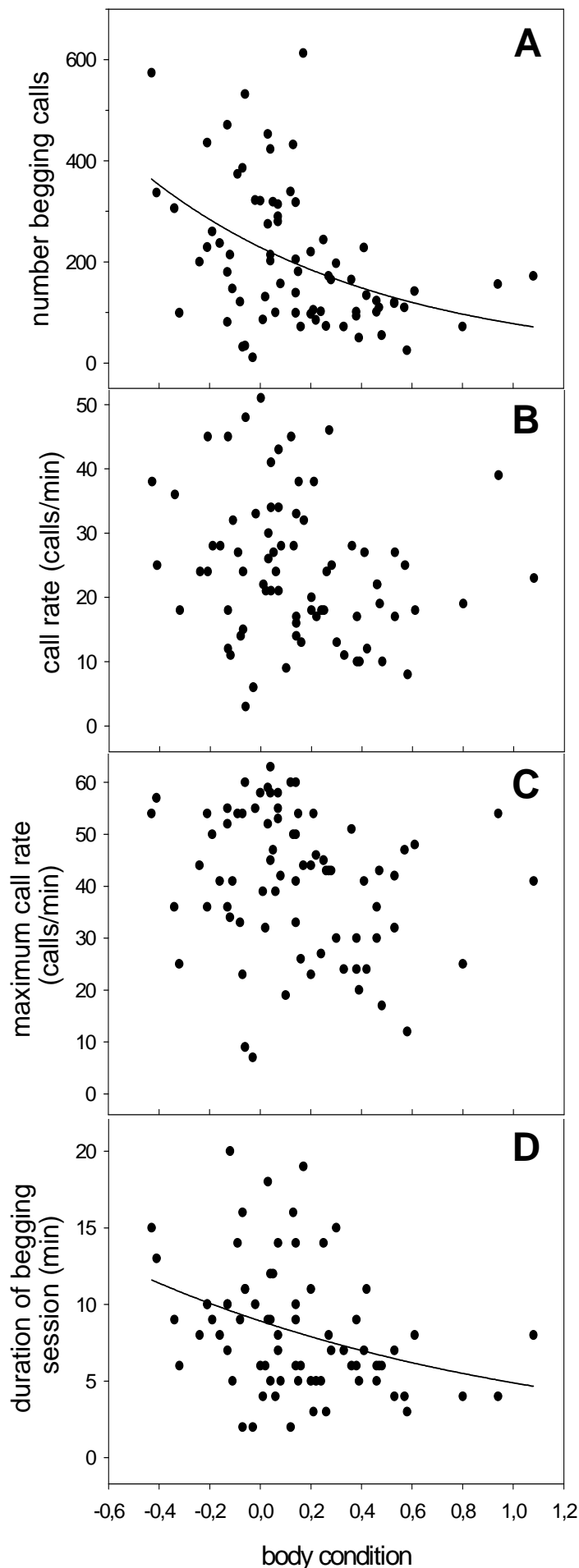
According to the relationships found for the sonographic call features and chick sex, the PCA factor related to the position of the maximum amplitude was the only one which showed sex specificity (ANOVA for factor 4: $F_{66} = 10.66$, $p = 0.002$). Female nestlings had significantly higher values of factor 4 than males.

Except the factor related to the location of maximum frequency, the other three PCA factors showed significant between-chick variability (ANOVA for factor 1: $F_{27} = 14.38$, $p < 0.001$; factor 2: $F_{27} = 4.32$, $p < 0.001$; factor 3: $F_{27} = 1.38$, $p = 0.15$; factor 4: $F_{27} = 2.80$, $p < 0.001$).

3.5. Influence of body condition

3.5.1. Body condition and the classic call parameters

The number of long begging calls and the duration of the begging session was significantly influenced by the chick's body condition. Nestlings in inferior state uttered more calls (ANOVA, $F_{77} = 10.059$, $p = 0.002$, Fig. 3.3.A) and extended the duration of the



begging session ($F_{77} = 4.993$, $p = 0.028$, Fig. 3.3.D). An increase in overall and maximum call rate with lower body condition was not statistically significant (call rate: $F_{78} = 1.072$, $p = 0.304$; maximum call rate: $F_{78} = 0.744$, $p = 0.391$).

By testing each season separately, slight differences arose. In 2005 none of the relationships between chick's body condition and classic call parameters were significant (number of long calls: $F_{43} = 2.220$, $p = 0.144$; call rate: $F_{43} = 0.147$, $p = 0.703$; maximum call rate: $F_{43} = 0.512$, $p = 0.478$; duration: $F_{43} = 1.016$, $p = 0.319$).

On the other side in 2006 the amount of begging calls ($F_{34} = 14.898$, $p < 0.001$), the duration of begging session ($F_{34} = 6.252$, $p = 0.018$) and moreover, the maximum call rate ($F_{35} = 5.469$, $p = 0.026$) were directly influenced by the chick's nutritional state. Only on the overall call rate the body condition had no effect ($F_{34} = 2.237$, $p = 0.144$).

Fig. 3.3. Relationship of the four classic call parameters and chick's body condition: number of begging calls (A), overall call rate (B), maximum call rate (C) and duration of the begging session (D). Regression curves are given where the correlation revealed significance (A, D).

3.5.2. *Body condition and sonographic call features*

Among the eleven parameters of the acoustic structure of begging elements, four were verifiably influenced by chick's body condition. Nestlings in a bad shape intensified their begging behaviour by increasing the frequency (ANOVA for FMax: $F_{69} = 10.760$, $p = 0.002$; FMean: $F_{69} = 11.192$, $p = 0.001$, PeakFTot: $F_{69} = 12.033$, $p = 0.001$) and therefore steepened the slope from frequency maximum to the end (SIMaxEnd: $F_{69} = 7.819$, $p = 0.007$). All other sonographic call features did not change with chick's body condition, although the breadth of elements showed a tendency to broaden with lower body condition (BroadTot: $F_{69} = 3.289$, $p = 0.070$).

Like the classic call properties the sonographic call features were differently influenced by body condition in the two seasons. The location of peak amplitude and the corresponding frequency were in 2005 affected in that way, that the maximum volume was reached later in the course of the element (LMaxAmp: $F_{34} = 6.163$, $p = 0.018$; LMA_Abs: $F_{34} = 4.780$, $p = 0.036$), while the loudest frequency increased with lowered body condition (PeakFTot: $F_{34} = 5.871$, $p = 0.021$). In 2006 chicks in poor body condition elongated the call duration ($F_{35} = 4.888$, $p = 0.034$), reduced the frequency of individual calls (FMax: $F_{35} = 7.018$, $p = 0.012$; FMean: $F_{35} = 12.604$, $p = 0.001$; PeakFTot: $F_{35} = 18.477$, $p < 0.001$) and shifted the amplitude peak more to the beginning of the element (LMaxAmp: $F_{35} = 10.715$, $p = 0.002$).

3.5.3. *Body condition and PCA factors*

From the PCA extracted factors the one strongly related to frequency showed an influence of body condition (ANOVA for factor 1 (both years): $F_{69} = 9.400$, $p = 0.003$; factor 1 (only 2006): $F_{35} = 15.76$, $p < 0.001$). There was no relationship found for the factors 2 to 4 and body condition for the whole dataset. But factor 4 showed a tendency to increase with decreasing body condition in 2005 (factor 4: $F_{34} = 4.228$, $p = 0.048$).

3.6. Differences between first and second feeding events

3.6.1. *Differences in call features between first and second feeding event*

Overall, during the second feeding event in one night the chicks begged more intensely. The amount of long calls uttered per session, the call rate and the maximum call rate were

enhanced during the second feeding, but only the difference in call rate was significant (Paired sample t-test, $t_{29} = -2.070$, $p = 0.047$).

From the sonographic call features solely the relative location of the peak frequency differed significantly from 0.463 ± 0.019 in the first to 0.408 ± 0.016 in the second feeding event ($t_{23} = 2.728$, $p = 0.012$), i.e. it has been shifted towards the beginning of the call. All other acoustic call parameters did not change from first to second feeding session.

The third of the PCA factors showed a significant decrease in begging between first and second feeding event, indicating an alteration in the location of the peak frequency ($t_{23} = 2.318$, $p = 0.030$) which confirms the findings of the sonographic feature analysis.

3.6.2. Differences in provisioning parameters between first and second feeding event

There were no recognizable changes in meal size (Paired sample t-test, $t_{29} = -0.410$, $p = 0.685$) or number of food transfers ($t_{29} = 0.270$, $p = 0.789$), nor in the duration of the feeding event ($t_{29} = 1.018$, $p = 0.317$) although the first feeding session seemed to last longer than the second (7.46 min versus 6.54 min).

3.7. Influence of supplementation on chick body condition and call features

Variations in chick body condition between control and treatment period were not caused by the supplementation (Repeated Measurements ANOVA, $F_{18} = 0.326$, $p = 0.589$).

Several effects were detected after the experimental provision with cod liver oil. Supplementary fed chicks had the tendency to reduce the call rate and to prolongate the duration of begging session, although these findings were significant only within one season, respectively (Fig. 3.4., Appendix A). The increase of the number of long begging calls during the treatment period was significant in 2006. No change was found in the maximum call rate sustained for one minute.

The experiment showed a very distinct influence on the sonographic call features (Fig. 3.4., Appendix A). In the combined dataset for both seasons chicks significantly reduced the frequency parameters FMax, FMean and PeakFTot during the treatment period. These effects were mainly derived from changes in the acoustic call parameters in 2005, while in 2006 none of those were significantly correlated with the treatment procedure. Beyond the impact on the frequency, the length of a single begging call, as well as the absolute time span until the peak amplitude was reached, shortened and SIMaxEnd

decreased, i.e. the slope from peak frequency to the end became more precipitous in the first season after chicks received supplemental food.

Only PCA factor 1 was statistically significantly influenced by the supplementation in 2005 which contributed to a similar result regarding the combined dataset of both seasons (Fig. 3.4., Appendix A). The analysis of the other PCA factors revealed no further correlation, although factor 2 had a marginal tendency to decrease from control to experimental treatment. Since there was no influence from supplemental feeding on the acoustic call parameters, it was not surprising to find no change in any of the PCA factors in 2006.

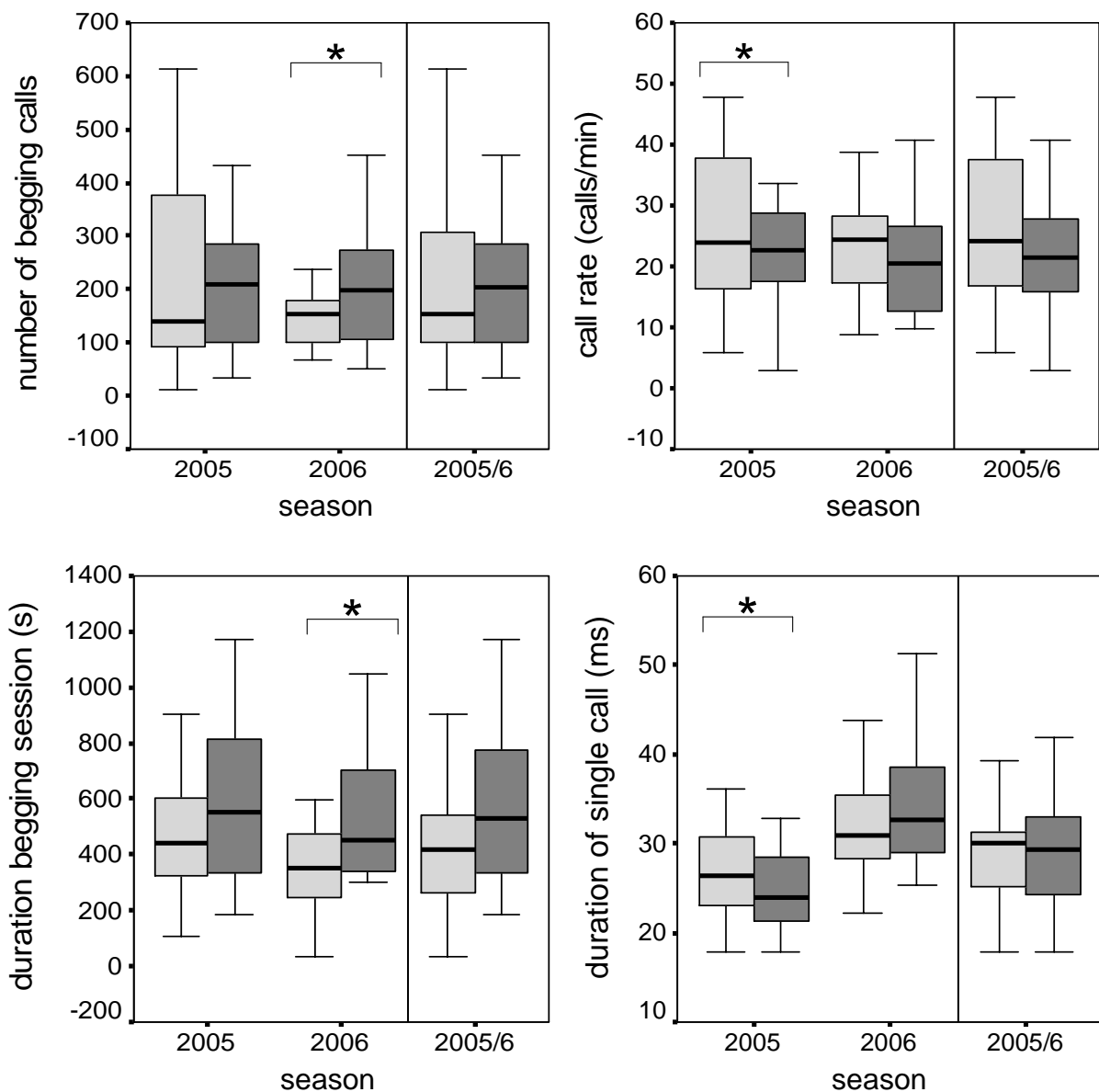


Fig. 3.4. Changes of different call parameters between control (light grey) and treatment period (dark-grey). The seasons are diagrammed sole and as combination of both years (2005/6). Only features where the GLM revealed at least in one season significant differences are presented as boxplots.

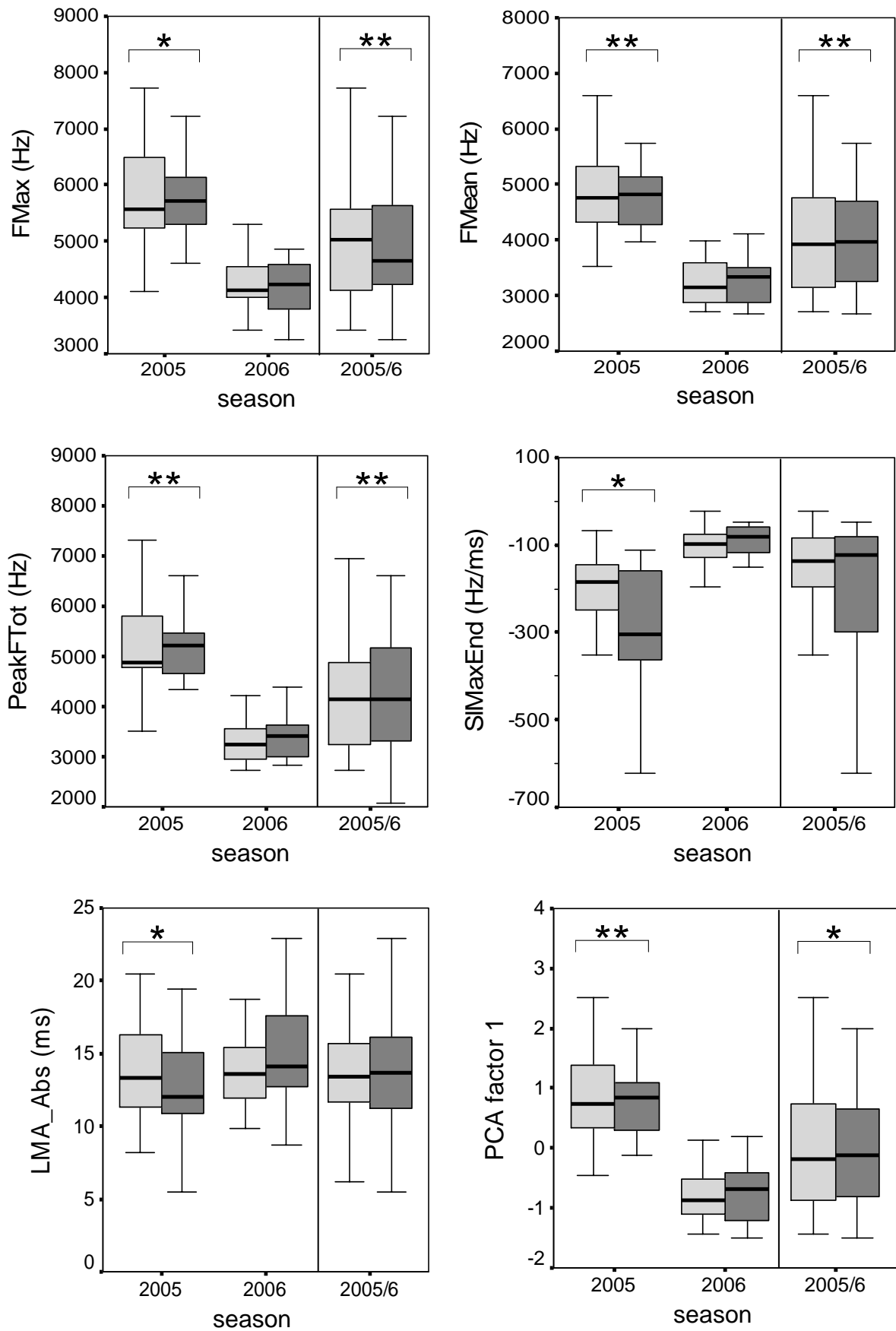


Fig. 3.4. (continued) Changes of different call parameters between control (light grey) and treatment period (dark-grey). The seasons are diagrammed sole and as combination of both years (2005/6). Only features where the GLM revealed at least in one season significant differences are presented as boxplots.

3.8. Parent – offspring interactions

3.8.1. Body condition and provisioning

The chick's body condition profoundly influenced the meal size provided by the parents (ANOVA $F_{75} = 14.85$, $p < 0.001$) and likewise the number of food transfers during one feeding event ($F_{77} = 4.262$, $p = 0.042$). Chicks in inferior body condition received more food than well nourished nestlings by means of more food transfers during one feeding session. To provide more food needed more time, so the overall duration of feeding also increased with lower nestling state ($F_{77} = 6.272$, $p = 0.014$).

3.8.2. Influence of call parameters on provisioning

No effect on the meal size was found for any of the classic call parameters (Tab. 3.5.), but the differences between the particular nests were marginally significant. Though individual differences also influenced the number of food transfers from adult to chick, an effect of the number of long calls uttered and the overall call rate on the quantity of food transfers was obvious as well. An intensification of begging, i.e. more numerous begging

Tab. 3.5. GLM of the influence of the classic begging call parameter on different provisioning variables. Only data of the control period were included, nest acted as fixed factor. Statistical significant P – values are marked bold.

Source	d.f.	F	P
Meal size			
Number of long calls	1	0.097	0.758
Call rate	1	1.518	0.229
Maximum call rate	1	2.664	0.114
Duration of begging session	1	0.509	0.482
Nest	24	1.920	0.051
Total	56		
Food transfers			
Number of long calls	1	7.829	0.009
Call rate	1	6.609	0.016
Maximum call rate	1	1.925	0.177
Duration of begging session	1	0.004	0.950
Nest	24	3.534	0.001
Total	56		
Duration of feeding session			
Number of long calls	1	7.689	0.010
Call rate	1	8.500	0.007
Maximum call rate	1	4.552	0.042
Duration of begging session	1	0.099	0.756
Nest	24	1.508	0.151
Total	56		

calls and an increase in the call rate led to an augmentation of food transfers and extended the feeding session. An enhanced maximum call rate also contributed to an increase in the time span of the feeding event.

The separate analysis of each season was less compelling. In 2005 the call rate was the only parameter which affected the duration of the feeding session ($F_{29} = 6.722$, $p = 0.027$), while individual differences caused changes in the number of food transfers ($F_{14} = 3.059$, $p = 0.041$). The number of long calls and the call rate influenced the quantity of food transfers in 2006 (call number: $F_{27} = 5.314$, $p = 0.038$; call rate: $F_{27} = 6.442$, $p = 0.025$). Like in the combined dataset, these call features were in all cases positively correlated to the provisioning variables.

Among the acoustic call features the impact on the meal size was more pronounced. The length of a single begging call ($F_{54} = 6.874$, $p = 0.018$) and the absolute location of maximum frequency (LFMaxAbs: $F_{54} = 5.572$, $p = 0.030$) had a significant influence on the meal size. Its relative counterpart LocFMax ($F_{54} = 4.378$, $p = 0.052$) and the peak frequency ($F_{54} = 3.381$, $p = 0.083$) showed at least a similar tendency. Nestlings received larger meals by elongating individual begging calls, shortening the time period until peak frequency was reached during a call element and by increasing the maximum frequency. More numerous food transfers ($F_{51} = 4.735$, $p = 0.046$) and a prolonged feeding session ($F_{50} = 5.491$, $p = 0.034$) were observed when BroadTot decreased. Furthermore, the duration of feeding session was influenced by the between-chick-variability ($F_{24} = 4.069$, $p = 0.004$).

The distinct GLM of the 2005 season revealed significant relations between slope parameters and the duration of the feeding event (SIStMax: $F_{25} = 17.02$, $p = 0.026$; SIMaxEnd: $F_{25} = 11.91$, $p = 0.045$). Steepened slopes, either from beginning to the peak frequency or from peak to the end of the call, resulted in a longer feeding session. Again, this time span was also influenced by the individual variability (Nest: $F_{14} = 14.51$, $p = 0.024$). In 2006 no effects on provisioning was found for any of the sonographic parameters.

An increase in PCA factor 2 led to an extension in provisioning time ($F_{50} = 6.100$, $p = 0.022$). The high between-chick-variability in PCA factors contributed to differences in duration of feeding ($F_{24} = 4.900$, $p < 0.001$) and number of food transfers ($F_{24} = 3.129$, $p = 0.005$), but not to meal sizes ($F_{25} = 1.380$, $p = 0.217$). The GLM for each season separately revealed that factor 2 had a marginal effect on the duration of feeding session in 2006 ($F_{25} = 4.202$, $p = 0.062$). However, significant was only the influence of nest on duration of feeding session both in 2005 ($F_{14} = 4.170$, $p = 0.044$) and 2006 ($F_9 = 4.202$,

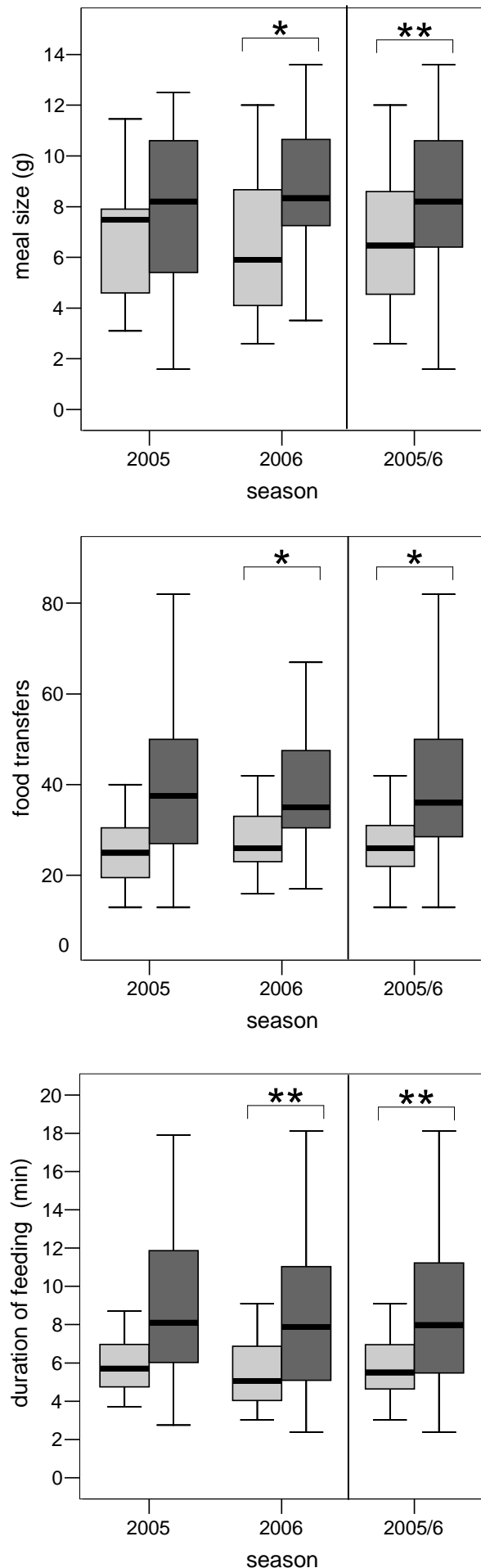
$p = 0.014$) and on the number of food transfers in 2005 ($F_{14} = 4.305$, $p = 0.030$). Variations in PCA factors 1, 3 and 4 did not result in any detectable alteration of provisioning.

3.8.3. Influence of supplemental feeding on provisioning

During the treatment period nestlings experienced significant enhanced provisioning by their parents (Fig. 3.5.). Meal sizes increased in first feeding events about one third from 6.32 ± 0.44 g to 8.27 ± 0.49 g ($F_{76} = 7.349$, $p = 0.009$). Food transfers and duration of feeding after supplementation exceeded the control period with 37.66 ± 2.81 to 27.74 ± 2.27 transfers ($F_{74} = 5.787$, $p = 0.020$), respectively 9.50 ± 1.11 min to 6.12 ± 0.40 min ($F_{74} = 8.265$, $p = 0.006$). There was no effect of nest on the amount of food provided. The feeding frequency was slightly reduced during the treatment period (1.32 ± 0.08 feeding visits per night compared to 1.45 ± 0.08 during the control period), though this difference was not significant ($F_{76} = 1.501$, $p = 0.227$).

No significant changes were found in

Fig. 3.5. Changes of provisioning between control (light grey) and treatment period (dark-grey). The seasons are diagrammed sole and as combination of both years (2005/6). Only first feedings per chick-night were included.



second feeding events, although the quantity of transfers and the duration of feeding increased slightly after supplementation.

3.9. Sex specificity in provisioning rules

Female nestlings received slightly bigger meals than males both in one feeding event (7.03 ± 0.67 g versus 6.14 ± 0.69 g) and over the whole night (11.84 ± 1.19 g versus 9.67 ± 1.45 g). Furthermore, they needed longer to finish the feeding session (6.38 ± 0.47 min versus 6.05 ± 0.76 min), although possessing less food transfers (27.33 ± 1.92 versus 31.20 ± 4.56). Nevertheless, none of these differences were statistically significant (ANOVA for meal size per feeding event: $F_{40} = 1.620$, $p = 0.211$; meal size per chick-night: $F_{41} = 0.297$, $p = 0.589$; food transfers: $F_{40} = 1.231$, $p = 0.274$; duration feeding session: $F_{40} = 0.231$, $p = 0.634$).

When visits by males and females were treated separately, from males less food (6.06 ± 0.66 g versus 6.96 ± 0.69 g) was provided to the nestling during fewer food transfers (25.00 ± 2.48 versus 29.47 ± 3.74). Only the duration of the feeding session was longer within males than within females (5.94 ± 0.48 min versus 5.73 ± 0.59 min). But the ANOVA revealed for these findings also no significances (meal size: $F_{43} = 0.946$, $p = 0.337$; food transfers: $F_{43} = 1.063$, $p = 0.309$; duration: $F_{42} = 0.474$, $p = 0.495$).

The restricted sample size was inappropriate to check for differences in the response of male and female parents to supplementation of their offspring.

4. Discussion

4.1. Chick development

Growth patterns, feeding frequencies and sizes of meals delivered to chicks were comparable to those recorded in previous years for Wilson's storm-petrels (Quillfeldt & Peter 2000; Quillfeldt 2001; Büßer et al. 2004; Gladbach 2005), indicating that collection of data had no harmful effects. Nevertheless, the two seasons investigated here display apparent variations in chick development, parental investment and overall breeding success. Furthermore, growing up in an experimental film nest did not affect growth of the chicks either. Increased handling due to the recording procedure occurred only in a short time span of the nestling period. Thus it was not expected to influence development, neither positive by means of higher food supply through supplementation (Bolton 1995a; Schmoll 2000), nor negative because chicks get accustomed to regular handling (Quillfeldt & Möstl 2003).

The main factors threatening Wilson's storm-petrels specified Quillfeldt (2001) to be low krill abundance and adverse weather conditions, snow storms in particular, causing high egg and chick mortalities. In 2006 feeding frequencies were higher and fewer chicks died from starvation, which provides indirect evidence that the pressure of food availability as a limiting factor was less severe in the second season than in the first. High wind speed in the second half of February and low temperatures at the beginning of March 2005 (compare Fig. 2.3.) might have been further impairment to the birds, as Bolton (1995b) mentioned for wind speeds exceeding 38 km/h a reduced foraging efficiency of Storm-petrels (*Hydrobates pelagicus*), an in size and foraging habits similar seabird. Differences in chick body development seem to reflect that the conditions posed a greater challenge to the storm-petrels in 2005 than in 2006. Growth rates of body mass, wing and primary feather in 2005 exceeded those in 2006, but growth stopped at lower (body mass and wing) or similar (tarsus and eighth primary) peak values. This is uncommon in two different respects.

First, nestlings of the Thin-billed prion (*Pachyptila belcheri*) growing up under low food availability rather decelerated their growth but reached normal tail and wing lengths due to an elongated fledging period (Quillfeldt et al. 2007a). Although fledging occurred after termination of the field season and therefore the exact date is unknown, a lengthening of the fledging period is unlikely because the breeding season of Wilson's storm-petrels in these high latitudes is restricted by the short summer and incipient adverse weather

conditions at the end of March (Obst & Nagy 1993; Quillfeldt & Peter 2000; Büßer 2003; Hodum & Weathers 2003). It rather seems as though low quality chicks are forced to leave the nest as soon as possible to start foraging by themselves in areas of potentially higher food availability, even under the constraints of being in a lower developmental state with less resources and consequently reduced changes of postfledging survival (Gaston 1997; Quillfeldt & Peter 2000). Remaining in the nest under these circumstances would represent certain death to the chick, whereas departure could be rewarded by survival (Oyan & Anker-Nilssen 1996).

Second, growing chicks facing shortage of food may preferentially allocate resources to characters of greatest importance for survival. Those were marked to be skull, wing and body mass (amount of subcutaneous fat, but not internal fat deposits) since these characters were least affected by variation in nutrition (Hudson 1979; Oyan & Anker-Nilssen 1996; Gjerdrum 2004). This does not coincide with the data of enhanced wing growth in 2005, unless the results are interpreted as following. Given relatively good conditions at the beginning of the chick rearing period, nestlings grew at a normal rate. With ongoing season, reduction of food availability would affect growth negatively. A change in resource allocation occurs to maintain wing growth at normal or even higher rates to ensure at least sufficient wing development in case conditions deteriorate further and nestlings need to leave the nest earlier than expected to avoid entombment by snow. This would explain the higher growth rates of wing and eighth primary and the lower wing length asymptote in 2005 compared to the more favourable season (2006). Besides breeding success, chick growth rates, body condition and feeding rates, also differences in the sonographic call features implicate that the breeding season 2006 was better in terms of food availability and weather conditions.

The influence of the hatching date on growth patterns is concordant to those reported by Wasilewski (1986) and Quillfeldt & Peter (2000). Later hatched chicks had a more rapid development in early life but ended up at lower peak masses and wing length asymptotes, an adaptation to the restricted breeding season.

No differences in development were detected regarding the chick's sex which is in line with neither male nor female nestlings should have higher energetic requirements since adult Wilson's storm-petrels do not differ, respectively only slightly, in body size (Büßer 2003; Gladbach 2005).

4.2. Honest signalling of need

Theory of honest signalling predicts that acoustic and behavioural components of begging function as reliable indicators of nestling's state (e.g. [Godfray 1995b](#); [Iacovides & Evans 1998](#); [Sacchi et al. 2002](#)). But theoretical approaches are difficult to evaluate without more detailed information on the structure and function of the various elements of begging displays, especially on which components nestlings encode information of need.

An increased number of begging calls or a higher call rate was found to correlate with nestling's hunger level in several song birds, e.g. American robins *Turdus migratorius* ([Smith & Montgomerie 1991](#)), Yellow-headed blackbirds *Xanthocephalus xanthocephalus* ([Price & Ydenberg 1995](#)), Tree swallows *Tachycineta bicolor* ([Leonard & Horn 2001b](#)), Barn swallows *Hirundo rustica* ([Sacchi et al. 2002](#)) and also in some Procellariiformes like Manx shearwater *Puffinus puffinus* ([Quillfeldt et al. 2004](#)) and Cory's shearwater *Calonectris diomedea* ([Quillfeldt & Masello 2004](#); [Trager et al. 2006](#)). Likewise, for Wilson's storm-petrels [Quillfeldt \(2002a\)](#) identified the number of long calls and the call rate of a begging session, but not its duration, as indicators of chick's body condition. [Sacchi et al. \(2002\)](#) mentioned that not only the frequency of performance of begging display, but also the call structure potentially reveals nestlings' need of food. In fact, needier nestlings uttered calls at higher frequency ([Leonard & Horn 2001a](#); [Gladbach 2005](#)) or amplitude ([Price & Ydenberg 1995](#)). These findings correspond quite well with the results of the present study. Lower nutritional state was found to be expressed by increasing numbers of begging calls uttered at high sound frequency during elongated begging sessions. Furthermore, high energy frequencies of begging calls (PeakFTot) were lower in heavy nestlings compared to light ones. This is supported on the basis of physical constraints linking tone pitch to body size in birds ([Morton 1977](#); [Ryan & Brenowitz 1985](#)).

It could have been shown that classic call components, the number of long calls in particular, encode the body condition of chicks. But this information is not transmitted until the begging session comes to an end. [Gladbach \(2005\)](#) mentioned that chicks utter calls during a feeding event as long as they are hungry, but stop calling as soon as they are satiated. The feeding adult should therefore finish provisioning by the time its offspring falls silent. My observations reveal a different picture. When the parent remains inside the nest burrow nestlings usually continued their calling, even though feeding already finished. Chicks should know that parents, once stopped provisioning, do not respond to solicitation behaviour anymore in one night. Why then do chicks deteriorate their resources and

continue calling? The sense of this vague behaviour might be rooted in providing an easily obtainable signal of need parents use to adjust their provisioning not in the current but in the next feeding event.

Regarding begging intensity and chick's state, results in the two seasons were not equally compelling. In 2005 few of the call parameters could be linked to the body condition, although they already achieved an advanced level of intensity. In this season of low food availability, begging probably reached a limit where it cannot be intensified further due to physical constraints even though offspring's needs escalate (Sacchi et al. 2002). For example the call rate might be restricted, giving chicks time to swallow food in between (Quillfeldt & Masello 2004). From this view the conclusion is drawn that chicks of high and medium body condition communicate their need with a gradual increase of begging intensity while low state nestlings convey their high food requirements without any nuances (Fig. 4.1.). This is plausible supporting that average and well-fed nestlings provide a graded signal so that parents might balance their decision about investment of limited resources accordingly. The calls of undernourished chicks, on the other hand, resemble an alarm signal of imminent starvation where no detailed information is needed. When body state declines further and undergoes a certain threshold, chicks are too weak to maintain the costs of begging anymore. Thus the intensity falls abruptly. Consequently, only in good seasons, respectively among non-starving nestlings, the variation in begging

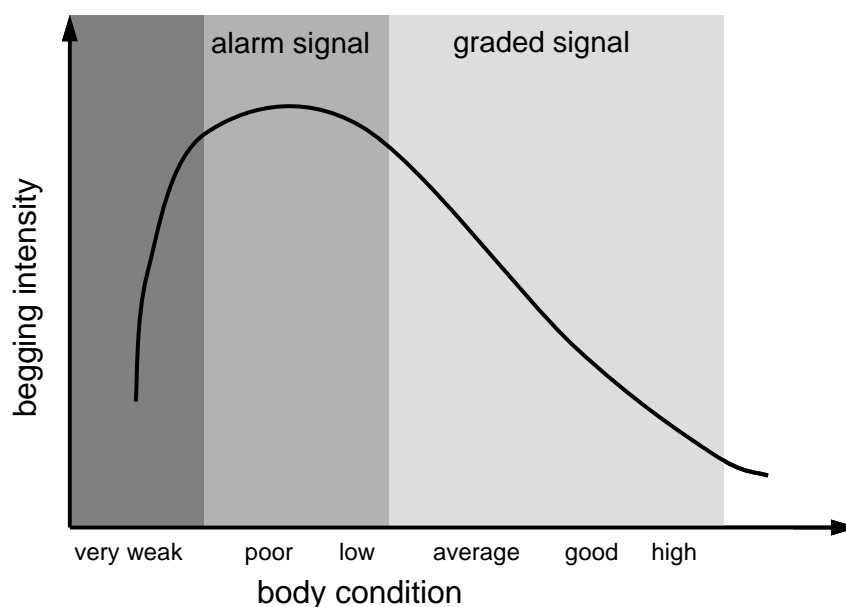


Fig. 4.1. Proposed progression of the intensity of a begging feature, costly classic call parameters in particular (e.g. number of long calls during a begging session), depending on chick's body condition. A linear incidence provides the base for a graded signal of nestlings in average and good condition (light grey area). Poor nestlings beg at the upper intensity limit, without differentiation (medium grey area). The dark grey area marks the range where chicks are too weak to maintain the high begging intensity.

might be large enough to be detectable (Quillfeldt & Masello 2004). However, the **prediction (1)** of different begging components changing with chicks' body condition and thus serve as a reliable signal of need, has been **verified** therewith.

The aim of a signal is to transmit information, which a recipient perceives and acts upon. Therefore the ability to distinguish details chicks communicate about their state was expected to coevolve accordingly (e.g. Guilford & Dawkins 1991; Rowe 1999). Evolution should favour those parents which optimize resource allocation with respect to their own fitness and that of their offspring (Harper 1986; Hussell 1988). Regarding this assumption, a great deal of attention has been directed to seabirds (e.g. Harris 1983; Johnsen et al. 1994; Wernham & Bryant 1998). For Grey-headed albatrosses (*Thalassarche chryostoma*) Phillips & Croxall (2003) provided experimental evidence that parental foraging efficiency and offspring demand are equally important for the regulation of provisioning. With some exceptions (Ricklefs 1987; 1992), albatrosses and petrels that feed their offspring every 1-3 days seem able to respond to variability in chick condition (Bolton 1995a; 1995b; Takahashi et al. 1999b; Weimerskirch & Lys 2000; Weimerskirch et al. 2003), while adult shearwaters cannot or do not respond to their offspring's immediate nutritional need (Hamer & Hill 1993; 1994; Hamer 1994).

In the present study of Wilson's storm-petrels, parameters of provisioning were found to be adjusted in accordance to chick's body condition. This is in line with former investigations (Quillfeldt 2002a; Gladbach 2005). Unfortunately, individual call parameters indicating body condition correlated only weakly with provisioning rates. Vice versa, call parameters significantly changing with meal size, number of food transfers or the duration of the feeding session, showed only marginal correlation or no connection at all to chick's body condition. There are two possibilities how parents might extract the information given during begging. Firstly, the signal is redundant, i.e. parents may rely on information obtained from two or more different call components to gain a better estimate of a single aspect of chick's condition, e.g. its short-term needs (*redundant signal hypothesis*, Møller & Pomiankowski 1993, Johnstone 1996). Those components might be the number and rate of long calls, their duration and frequency breadth. These call characters changed most with provisioning. In this case the weak correlation from body condition with these call features is effectual due to the recurrence of the information in every of the four call components.

The second and more likely possibility implies that the begging display carries multiple messages providing information about different aspects of chick condition or quality

(*multiple signal hypothesis*, Johnstone 1995; 1996; Christe et al. 1996; Leonard & Horn 2001a). Call parameters indicating body condition do not inevitably need to correlate with supply rates since adults should consider several aspects of chick's state (e.g. nutritional condition, age, immunocompetence, parasite infestation) and thus different call parameters for decision making. The number of long calls, the duration of a begging session and the pitch of call elements seem to contribute to this multiple solicitation signal. Certainly, there are more features of the begging display involved, than the ones selected for this study. Signals with multiple components, especially those in different sensory modalities, improve detection and discrimination by receivers (Rowe 1999; Rowe & Skelhorn 2004). Thereby the information is not only encoded in the individual begging component but certain combinations may interact in different ways. In a study of the reed warbler (*Acrocephalus scirpaceus*) Kilner et al. (1999) demonstrated that parents integrated visual and vocal signals from their young to adjust provisioning rates since the two signals conveyed more accurate information than either did alone. Visual signals like the presentation of brightly coloured gapes (Heeb et al. 2003) are inappropriate for Wilson's storm-petrels due to the lack of illumination in the nest burrows, particular at night when feeding occurs. Therefore parents might not be able to perceive any visual cue. One possible non-vocal stimulus may be the tactile beak pecking nestlings perform during solicitation behaviour (e.g. Miller & Conover 1983). Further research is needed to evaluate the contribution to the information transmission between parents and their offspring of this and other behavioural components.

Although the complex interplay of solicitation behaviour and parental response is not yet decoded in all its particulars, it was demonstrated that parents are able to perceive the information provided by their chicks and that they base their feeding decisions accordingly. Therefore the **second prediction** is also **verified**.

4.3. Does supplementation affect chick's honesty?

Providing additional food was expected to improve chick's nutritional state. Hence intensity of begging parameters indicating body condition and subsequently provisioning rates should have been reduced as reported from other supplementary feeding experiments in seabirds (e.g. Bolton 1995a; Harding et al. 2002; Quillfeldt & Masello 2004; Hamer et al. 2006). By contrast, in this study adults attending chicks during the treatment period exhibited a significant increase in their average nightly food delivery by about one-third.

During this time span experimental chicks thus received extra food from two sources (artificial and parental). Although unexpected, these results further support the second prediction, because parents just responded to intensified begging of their supplemented chicks.

For adjusting provisioning rates parents have three possibilities. Either they alter the frequency of returns to the colony with food (Cook & Hamer 1997; Hamer et al. 1998; Gjerdrum 2004), maintain the feeding frequency but change the meal size provided per visit (Weimerskirch et al. 2000; Hamer et al. 2006) or modify the composition of the prey delivered (Grieco 2001). Surely, combinations of these strategies occur as well (e.g. Weimerskirch et al. 1997b). The most efficient and thus common strategy is to attend the breeding site less often when food demand at the nest is low to save energetic costs (Ydenberg 1994) and avoid the high predation risk at the colony (e.g. Mougeot et al. 1998). In Wilson's storm-petrels regulation of food delivery appears to operate at the level of feeding frequency since this value is more variable among the seasons than the amount of food provided per nest visit (c.f. Schmoll 2000; Büßer et al. 2004). The capacity of carrying food is closely restricted to their small body size. Astonishing is that during supplementation parents delivered larger meals although maintaining their nest attendance rate. Hence the question arises if parents provide all food to the nestling or if they retain a certain amount as buffer. According to Ricklefs (1992) Leach's storm-petrels (*Oceanodroma leucorhoa*) deliver their whole stomach content carried back to the colony. But how then do parents adjust their provisioning to chick's nutritional state? This scenario would imply that adults know their offspring's need two or three nights in advance, at the previous feeding visit. Although body condition is not independent from chick's former state and thus might be extrapolated, it also depends heavily on the recent feeding history (this study; Wright et al. 2002). Pair partners feed their nestling independent from each other, so it seems unlikely to assess chick's requirements beforehand. Therefore I rather suggest that returning parents carry a relatively constant amount of food to the nest where offspring communicates its current needs and receives provision accordingly. Depending on chick's need at the last feeding visit (communicated through the classic call parameter) and under the constraints of prevailing food availability parents might roughly balance their provisioning rate via changing feeding frequency, while fine tuning of provided meal size occurs during chick feeding (mediated mainly by sonographic call features). This is in line with the observation that Wilson's storm-petrels ad hoc increased the meal size provided to supplemented chicks due to intensified begging without altering their feeding frequency.

Though provisioning can readily be decreased, its enhancement above a certain level is restricted by the capacity of the birds to carry food and, of course, resource availability. This implication is drawn from the inability of parents to increase provisioning rates due to intensified begging of manipulated nestlings in 2005. Similar results of adults failing to respond to an experimental increase in food demand at the nest but reducing provisioning when offspring is in appropriate state, were already reported from songbirds (Siikamaki et al. 1998; Saino et al. 2000), other tubenoses (Weimerskirch et al. 1997b; Hamer et al. 1999; Takahashi et al. 1999b) and auks (Johnsen et al. 1994; Hipfner et al. 2006). The adjustment of parental provisioning rates to chicks needs seem to be restricted to ample food availability, whereas periods of scarce environmental conditions may give adults little leeway to extend their foraging effort to improve the state of poorly nourished chicks.

Nevertheless, I failed to show that supplementation results in a decrease in the chicks begging intensity and reduced provisioning by the adults. Therefore I need to **reject the third prediction**. Why supplemented chicks increase their begging effort still lacks an explanation. Statistically there was no difference in the body condition of chicks between control and treatment periods albeit intensified begging indicated a lowered nutritional state after manipulation. This might be due to parents countervailing the increased demand of their offspring by providing larger meals before it could have been deposited in a decreased body condition.

To my knowledge, Mock et al. (2005) are the only ones, reporting similar observations derived from a supplemental feeding experiment in house sparrows (*Passer domesticus*), i.e. an increase in the provisioning rate of adults to their supplemented offspring. Since the authors did not take the begging behaviour of nestlings into account, they could only suspect supplemented broods to beg more intensely due to a preliminary (but unpublished) study. Consequently, the provided model of parents perceiving their supplemented chicks as high-quality offspring and thus invest more than average, while chicks in unusual good condition intensify their begging, is at odds with the view that solicitation behaviour is an honest indicator of neediness (Godfray 1991; Kilner & Johnstone 1997).

However, I suggest my findings to be rather the product of a true parent – offspring interaction, than of methodical shortcomings. Even under control conditions nestlings changed some of their call components from first to second feeding events in one night. For one parameter, the overall call rate, this was already reported from an empiric investigation of Wilson's storm-petrels (Gladbach 2005). In the following I will discuss two hypotheses, the *activation* and the *balance hypothesis*, to, a posteriori, propose

proximate causes of the intensification in solicitation behaviour of Wilson storm-petrel nestlings after receiving additional food.

Firstly, undisturbed nestlings seem to doze most of the time in the nest. The handling for applying supplementation, respectively the first feeding per night of unmanipulated controls by their parents might rouse chicks from this lethargy. By receiving food, either artificial or parental, they activate their basal metabolism to cope with the increased food availability which in turn influences their requirements positively. Consequently their readiness to beg in the next provisioning event of the same night increases (c.f. [Sacchi et al. 2002](#)). Food thus serves as a kind of appetizer, especially when only a small amount was delivered which does not satiate the chick completely (*activation hypothesis*). This would be in line with the observation of increased begging in second feeding events of unmanipulated nestlings in this and a former study ([Gladbach 2005](#)). Differences in the digestive ability between control and supplemented nestlings were also mentioned by [Takahashi et al. \(1999b\)](#) for Leach's storm-petrels. In their investigation supplemented chicks experienced a higher mass loss rate than controls during the daytime. This can be traced back to an enhanced (activated) basal metabolism due to the supplementation treatment as suggested for my findings in Wilson's storm-petrels. But the authors themselves explain it with limitations of the assimilatory capacity of the digestive tract of chicks and thus an inability to assimilate all food they received ([Takahashi et al. 1999b](#)). We can rule out this possibility, at least for Wilson's storm-petrel chicks, since they can handle meal sizes of up to 26 g per night (receiving maximum meal sizes by both parents) smoothly. Therefore an additional food supply of 2 g does not seem to cause any troubles.

Alternatively, the *balance hypothesis* is outlined: Cod liver oil is comparable to the stomach oil of Procellariiformes regarding the energy content, but it maybe lacks an essential, presumably water-soluble nutrient (a protein, water-soluble vitamin or mineral, e.g. calcium ([Taylor & Konarzewski 1992](#); [Schmoll 2000](#))). If nestlings perceive this disparity, they attempt to receive more proper food from their parents by intensifying their solicitation behaviour (c.f. [Thomas et al. 1993](#)). By requesting more provision they try to counterbalance the malnutrition arising from artificial supplementation. This second scenario would explain why the additional food, chicks get from parents during the treatment period, perfectly equals the amount of artificial food supplied. This argumentation of a missing essential nutrient in the cod liver oil, was already proposed by [Schmoll \(2000\)](#). He failed to show any differences in the growth of continuing supplemented Wilson's storm-petrel nestlings compared to unmanipulated controls,

although faster growth is one of the three most commonly reported short-term surrogates compiled by [Mock et al. \(2005\)](#).

Both hypotheses do have their rough edges and might not be able to explain the observation sweepingly, but they are not mutually exclusive. In the *activation hypothesis* supplemented nestlings deplete their resources more rapidly due to the increased basal metabolism and consequently have higher short-term requirements which they advertise. Underlying the *balance hypothesis*, manipulated chicks intensify the begging to satisfy their demand of a special nutrient. As a matter of fact, they also communicate a need. Thus neither of the two hypotheses does impair the view of begging display as an honest signal of need. Nevertheless, I rather support the first hypothesis and condemn the latter one. It seems unlikely that the cod liver oil, which is a commonly used supplement in several animal studies (e.g. [Chamberlain et al. 1991](#); [Schmoll 2000](#)) and even humans, should lack an essential nutrient. But I cannot rule out this possibility. On the other hand, the *activation hypothesis* might be corroborated with expertise from (human) physiology. Several hormones are known to suppress hunger symptoms (e.g. serotonin, leptin), while others (e.g. ghrelin) enhance it ([Bellisle et al. 1998](#); [Pliquet et al. 2006](#)). Mechanical and chemical stimuli of the stomach wall lead to the release of gastrointestinal hormones, like gastrin, which in turn cause the activation of digestive processes. Especially small amounts of food might activate the digestive tract but refuse to assuage the organism's requirements. Thus, resources allocated to production and release of hormones and digestive enzymes need to be refilled, causing an enhancement of need. Therefore I predict that the cause of increased metabolism and thus demand after supplementation of Wilson's storm-petrel nestlings might be found in this complex network.

4.4. Bias in parental care and responsiveness

Previous studies of passerines (e.g. [Christe et al. 1996](#); [Macgregor & Cockburn 2002](#); [Mock et al. 2005](#)) found unequal contribution in progeny feeding between male and female parents. This is commonly attributed to males benefiting less from providing parental care due to their lower certainty of paternity and broader opportunities for extrapair fertilizations (e.g. [Queller 1997](#); [Macgregor & Cockburn 2002](#)), or in monogamous (seabird) species to sexual dimorphism in body size ([Gonzalez-Solis et al. 2000](#); [Weimerskirch & Lys 2000](#)). Furthermore, female parental behaviour is more flexible and responsive to offspring requirements in some species ([Huin et al. 2000](#); [Kilner 2002](#);

Quillfeldt et al. 2004) but not in others (Christe et al. 1996; Schwagmeyer & Mock 2003). Whatever might be the reason for such differences in responsiveness between males and females, I did not expect to find any sex bias since Wilson's storm-petrels are both monogamous (Quillfeldt et al. 2001) and monomorphic (Büßer 2003; c.f. Peck & Congdon 2006). Thus males can be confident about parentage of their nestling and no disadvantages arise from being equally involved in caring. In fact, male and female parents contributed to chick provisioning to the same extent. This is **in line with prediction (4)** and former studies reporting equal nest attendance rates and food deliveries for both sexes (Büßer 2003; Gladbach 2005).

4.5. Conclusion and prospects

There is overwhelming evidence that begging and provisioning strategies in Wilson's storm-petrels depend heavily on prevailing food abundance during the breeding season. An adult arriving in the nest burrow uses the information that are apparently encoded in nestling begging behaviour to make optimal decisions on allocation of resources critical to their own fitness and that of their offspring. In very poor environmental conditions, chronically starving chicks beg constantly at the upper intensity limit, giving no scope for variation. At the same time adults may not be able to increase provisioning rates either. Under those conditions, parents should be selected to ignore the signal, conserving their own body condition to increase their survival prospects to the next potential reproductive period. In contrast, in times of higher food abundances, chicks beg at intermediate levels, providing a graded signal and parents readily adjust provisioning rates. To achieve a more detailed comprehension of which call parameters determine parental feeding decisions, a playback-experiment is needed. The separate modification of single acoustic components offers the possibility to identify the one, respectively the combination of call parameters, which prompt parents to adjust provisioning. Nevertheless, the between chick variability, which was considerably in almost every call parameter included in the present study, and environmental fluctuations still pose an important source of variance. Blurring arising from individuality might be overcome with more recurrences per nestling, but still needs to be taken into account.

Since in this study the focus was laid upon chick's performance, further studies should include aspects of adult condition (e.g. by determining mass loss or feather regrowth rates) to reach a better understanding of the part adults play in the observed patterns. Chaurand &

Weimerskirch (1994) and Weimerskirch et al. (2000) already mentioned that food availability, species foraging strategy, age, experience and the condition of the individual parent may influence parental behaviour and thus the outcome of such experiments.

Making information easy to detect, discriminate and remember by receivers will probably increase the success of a signal and would be selected for (Guilford & Dawkins 1991). The relationships found between need, begging call structure and provisioning in the present study have implications for how solicitation behaviour might be designed for effective transmission to parents. Call components found here chicks use to communicate their body condition (number of long calls, duration of begging session, sound frequency and duration of a single element) were not only similar to such found in other Procellariiformes, but also to those reported from a row of songbird studies (see chapter 4.2.). Hence, a ubiquitous pattern is suggested to underlie these findings. The pitch of a call, for example, might closely be related to the body size due to physical constraints and, thus, give parents an easy, but barely delusive, acoustic indicator for assessing offspring mass. Furthermore, the number of long calls and thus the duration of a begging session were assumed to provide the basis parents use to adjust their future provisioning effort to, e.g. the feeding frequency, instead of being involved in the current feeding event.

On first sight contradicting the honest signalling theory, intensified begging of supplemented chicks can be explained in its accordance. Providing additional food either aroused nestlings, resulting in an alteration of their metabolism (*activation hypothesis*), or caused an imbalance of nutrients (*balance hypothesis*). Both explanatory approaches end up assuming a lack of energy, respectively an essential nutrient, which is advertised by the chick. Though unexpected, these findings further support the idea of nestlings communicating their need honestly.

The initial goal to examine how nestling's need is encoded in the structure of begging calls of Wilson's storm-petrels, I state to be partly achieved. Some open questions still remain. Although I support the view that nestlings communicate their state as a *multiple signal*, I can not reject the *redundant signal hypothesis*. Likewise, further work needs to be done to reliably unscramble causes and evolutionary backgrounds of increased begging intensity after receiving food (*activation vs. balance hypothesis*).

5. Summary

Whether parents or their dependent offspring control provisioning and how resource allocation is mediated behaviourally are fundamental questions in the context of parent – offspring conflict. Pronounced begging display of nestlings commonly precedes and accompanies provisioning by parents and is widely seen as advertisement of food demand at the nest.

Vocalisations during feeding of chicks of a small long-lived seabird, the Wilson's storm-petrel (*Oceanites oceanicus*), were recorded on King George Island, maritime Antarctic, to evaluate their information content and effects on regulating provisioning by the attending adult. A supplemental feeding experiment was conducted in order to verify empirical findings.

During the control period chicks honestly signalled their nutritional need. They conveyed information about their body condition through the number and sound frequency of begging calls uttered during feeding sessions. Begging intensity increased with decreasing body condition, both within and between nestlings. Thus they provided a graded signal of need as long as being in an appropriate state. Escalation of necessity resulted in begging at the upper limits, where it could not be intensified further. Parents were responsive to the information communicated through solicitation behaviour and delivered larger meals to nestlings in a poorer state but within a certain range under the constraints of food availability.

Data suggest that parents might use classic as well as sonographic components of the begging display to adjust provisioning rates. The feeding frequency might be roughly based on the number of long calls of the last begging session, while the meal size depend mainly on sonographic parameters, e.g. syllable duration and pitch of calls uttered during the prevailing feeding. Nevertheless, evidences how chicks convey details of their body condition are ambiguous. Either single aspects of chick's needs are encoded in acoustic (number and sound frequency of long calls) components of the begging display (*multiple signal hypothesis*). In this case further sensory modalities might be involved (e.g. tactile beak pecking). Alternatively, the whole information is repeated in the number and rate of long calls, the element duration and frequency breadth (*redundant signal hypothesis*).

Adults attending artificial fed nestlings increased delivered meal sizes by 2 g, which equals one third of a usual feeding, as response to intensified begging of their supplemented chicks. Providing additional food either aroused nestlings, resulting in an alteration of their metabolism (*activation hypothesis*), or caused an imbalance of nutrients

due to the lack of an essential one (*balance hypothesis*). These two hypotheses are proposed to interpret the findings, but neither of them does interfere with the view of honest signalling in Wilson's storm-petrel nestlings.

6. Zusammenfassung

Zentrale Fragen des Eltern – Nachkommen Konflikts beschäftigen sich damit, wer hauptsächlich die elterliche Fürsorge kontrolliert, ob Altvogel oder der von ihm abhängige Nestjunge, und wie spezielle Verhaltensweisen die Verteilung beeinflussen. Allgemein wird angenommen, dass Küken dem Elternvogel ihre Bedürfnisse durch ausgeprägtes Bettelverhalten vor und während der Fütterung vermitteln. Der Informationsgehalt dieser Bettelrufe und ihren Einfluss auf die Regulierung der Futtermenge durch den fütternden Altvogel wurden an einem kleinen, langlebigen Seevogel, der Buntfußsturmschwalbe (*Oceanites oceanicus*), auf King George Island, maritime Antarktis, untersucht. Zur Evaluierung empirischer Daten wurde ein Zufütterexperiment durchgeführt.

Während der Kontrollphase signalisierten die Jungen ihren Futterbedarf. Anzahl und Dauer der Bettelrufe während einer Fütterung, sowie Frequenzparameter gaben eindeutige Hinweise auf die körperliche Verfassung des Kükens. Die Bettelintensität nahm mit sich verschlechternder Körperkondition eines Nestjungen ab. Dieser Zusammenhang konnte auch zwischen den Küken nachgewiesen werden. Solange ihr Ernährungszustand sich in einem normalen Rahmen bewegte, boten Küken ein ihren Bedürfnissen entsprechendes, abgestuftes Signal. Verschlechterte sich ihr Zustand jedoch zunehmend, erreichte die Bettelintensität eine Obergrenze, die nicht weiter gesteigert werden konnte. Altvögel reagierten auf die im Bettelverhalten kodierten Informationen, indem hungrierere Nachkommen mit größeren Futtermengen versorgt wurden. Dies geschah jedoch nicht unabhängig von der aktuellen Nahrungsverfügbarkeit.

Die Ergebnisse weisen darauf hin, dass Altvögel ihrem Fütterungsverhalten sowohl klassische, als auch sonographische Komponenten des Bettelns zugrunde legen. Die Häufigkeit, mit der sie zum Nest zurückkehren, scheint von der Anzahl der Bettelrufe während der letzten Fütterung abzuhängen, wohingegen die übergebene Futtermenge der Länge und Frequenz einzelner Silben angepasst wird. Details über die Art und Weise mit der Küken ihre Körperkondition mitteilen, bleiben weiterhin zweideutig. Einerseits können akustische (Anzahl der Rufe, Frequenz) Bettelparameter unabhängig voneinander über

unterschiedliche Aspekte informieren (*multiple signal hypothesis*). Eventuell spielen in diesem Zusammenhang auch weitere Sinnesmodalitäten eine Rolle (z.B. taktiler Schnabelpicken). Andererseits kann die gesamte Information in der Anzahl und Rate der Bettelrufe, sowie deren Länge und Frequenzspanne wiederholt dargeboten werden (*redundant signal hypothesis*).

Experimentell zugefütterte Küken erhielten von ihren Eltern 2 g mehr Futter. Das entspricht etwa 30% einer normalen Fütterung. Mit diesem Verhalten reagierten die Altvögel auf die erhöhte Bettelaktivität ihrer Jungen. Um diese Beobachtung zu erklären, werden zwei Hypothesen vorgeschlagen und diskutiert: Entweder führte das Zufüttern zu einer Erhöhung des Stoffwechsels, da es die Küken aus ihrem Dämmerzustand aufweckte (*activation hypothesis*) oder dem künstlich verabreichten Futter mangelt es an einem essentiellen Nahrungsbestandteil, der infolgedessen über die von den Eltern bereitgestellte Nahrung aufgenommen werden musste (*balance hypothesis*). Keine der beiden Hypothesen widerspricht jedoch der These, dass die Küken durch das Betteln ihre tatsächlichen Bedürfnisse anzeigen.

7. References

- Arctander, P.** (1988): Comparative Studies of Avian DNA by Restriction Fragment Length Polymorphism Analysis - Convenient Procedures on Blood-Samples from Live Birds. *Journal für Ornithologie*. **129**:205-216.
- Beck, J. R. and D. W. Brown** (1972): The biology of Wilson's Storm petrel, *Oceanites oceanicus* (Kuhl), at Signy Island, South Orkney Islands. *British Antarctic Survey Scientific Reports*. **69**:1-54.
- Bellisle, F., J. E. Blundell, L. Dye, M. Fantino, E. Fern, R. J. Fletcher, J. Lambert, M. Roberfoid, S. Specter, J. Westenhofer and M. S. Westerterp-Plantenga** (1998): Functional food science and behaviour and psychological functions. *British Journal of Nutrition*. **80**:173-193.
- Bertram, D. F., C. V. J. Welham and R. C. Ydenberg** (1996): Flexible effort in breeding seabirds: Adjustment of provisioning according to nestling age and mass. *Canadian Journal of Zoology-Revue Canadienne de Zoologie*. **74**:1876-1881.
- Bolton, M.** (1995a): Experimental evidence for regulation of food delivery to Storm Petrel, *Hydrobates pelagicus*, nestlings - the role of chick body condition. *Animal Behaviour*. **50**:231-236.
- Bolton, M.** (1995b): Food delivery to nestling Storm Petrels: limitation or regulation? *Functional Ecology*. **9**:161-170.
- Bradley, J. S., J. M. Cox, L. W. Nicholson, R. D. Wooller, K. C. Hamer and J. K. Hill** (2000): Parental influence upon the provisioning schedules of nestling Short-tailed Shearwaters *Puffinus tenuirostris*. *Journal of Avian Biology*. **31**:522-526.
- Bretagnolle, V.** (1996): Acoustic communication in a group of nonpasserine birds, the petrels. In: *Ecology and evolution of acoustic communication in birds*. Ed. by D. E. Kroodsma and E. H. Miller. Ithaca: *Cornell University Press*. pp. 160-177.
- Bunce, A.** (2001): Effects of supplementary feeding and artificial twinning on nestling growth and survival in Australasian Gannets (*Morus serrator*). *Emu*. **101**:157-162.
- Büßer, C.** (2003): Elterliche Investition und Morphometrie der Buntfußsturmschwalbe (*Oceanites oceanicus*) auf King George Island, Südshetland-Inseln, Antarktis. *Diplomarbeit Friedrich-Schiller-Universität Jena*. 70 pp.
- Büßer, C., A. Kahles and P. Quillfeldt** (2004): Breeding success and chick provisioning in Wilsons storm-petrels *Oceanites oceanicus* over seven years: frequent failures due to food shortage and entombment. *Polar Biology*. **27**:613-622.
- Chamberlain, J. G., L. E. Dittmann, S. Hunt, H. Olson and J. R. Cashman** (1991): Effects of Long-Term 2-Percent Fish Oil Supplements on Tissue Fatty-Acids, Phospholipids, Cholesterol, and Arterial Histology in Japanese Quail (*Coturnix coturnix japonica*). *Artery*. **18**:291-314.
- Chaurand, T. and H. Weimerskirch** (1994): The regular alternation of short and long foraging trips in the blue petrel *Halobaena caerulea*: a previously undescribed strategy of food provisioning in a pelagic seabird. *Journal of Animal Ecology*. **63**:275-282.

- Choi, I. H. and G. S. Bakken** (1990): Begging Response in Nestling Red-Winged Blackbirds (*Agelaius phoeniceus*) - Effect of Body-Temperature. *Physiological Zoology*. **63**:965-986.
- Christe, P., H. Richner and A. Oppliger** (1996): Begging, food provisioning, and nestling competition in great tit broods infested with ectoparasites. *Behavioral Ecology*. **7**:127-131.
- Clark, A. B. and W. H. Lee** (1998): Red-winged blackbird females fail to increase feeding in response to begging call playbacks. *Animal Behaviour*. **56**:563-570.
- Cook, M. I. and K. C. Hamer** (1997): Effects of supplementary feeding on provisioning and growth rates of nestling Puffins *Fratercula arctica*: Evidence for regulation of growth. *Journal of Avian Biology*. **28**:56-62.
- Cotton, P. A., A. Kacelnik and J. Wright** (1996): Chick begging as a signal: Are nestlings honest? *Behavioral Ecology*. **7**:178-182.
- Croxall, J. P., H. J. Hill, R. Lidstone-Scott, M. J. O'Connell and P. A. Prince** (1988): Food and feeding ecology of Wilson's storm petrel *Oceanites oceanicus* at South Georgia. *Journal of Zoology*. **216**:83-102.
- Dearborn, D. C.** (1999): Brown-headed Cowbird nestling vocalizations and risk of nest predation. *Auk*. **116**:448-457.
- del Hoyo, J., A. Elliott and J. Sargatal** (1992): Family Hydrobatidae (storm-petrels). In: *Handbook of the Birds of the World*. Barcelona: Lynx Edicions.
- Erikstad, K. E., M. Asheim, P. Fauchald, L. Dahlhaug and T. Tveraa** (1997): Adjustment of parental effort in the puffin; The roles of adult body condition and chick size. *Behavioral Ecology and Sociobiology*. **40**:95-100.
- Furness, R. W. and B. L. Furness** (1981): A technique for estimating the hatching dates of eggs of unknown laying date. *Ibis*. **123**:98-102.
- Gaston, A. J.** (1997): Mass and date at departure affect the survival of Ancient Murrelet *Synthliboramphus antiquus* chicks after leaving the colony. *Ibis*. **139**:673-678.
- Gjerdrum, C.** (2004): Parental provisioning and nestling departure decisions: A supplementary feeding experiment in Tufted Puffins (*Fratercula cirrhata*) on Triangle Island, British Columbia. *Auk*. **121**:463-472.
- Gladbach, A.** (2005): Begging behaviour of Wilson's storm-petrel (*Oceanites oceanicus*) and its effect on parental investment. *Diplomarbeit Friedrich-Schiller-Universität Jena*. 48 pp.
- Godfray, H. C. J.** (1991): Signaling of Need by Offspring to Their Parents. *Nature*. **352**:328-330.
- Godfray, H. C. J.** (1995a): Evolutionary-Theory of Parent-Offspring Conflict. *Nature*. **376**:133-138.
- Godfray, H. C. J.** (1995b): Signaling of Need between Parents and Young - Parent-Offspring Conflict and Sibling Rivalry. *American Naturalist*. **146**:1-24.
- Gonzalez-Solis, J., J. P. Croxall and A. G. Wood** (2000): Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. *Oikos*. **90**:390-398.

-
- Granadeiro, J. P., M. Bolton, M. C. Silva, M. Nunes and R. W. Furness** (2000): Responses of breeding Cory's shearwater *Calonectris diomedea* to experimental manipulation of chick condition. *Behavioral Ecology*. **11**:274-281.
- Grieco, F.** (2001): Short-term regulation of food-provisioning rate and effect on prey size in blue tits, *Parus caeruleus*. *Animal Behaviour*. **62**:107-116.
- Guilford, T. and M. S. Dawkins** (1991): Receiver Psychology and the Evolution of Animal Signals. *Animal Behaviour*. **42**:1-14.
- Gustafsson, L. and W. J. Sutherland** (1988): The Costs of Reproduction in the Collared Flycatcher *Ficedula albicollis*. *Nature*. **335**:813-815.
- Hahn, S.** (1997): Ökologische Untersuchungen am Schwarzbauchmeerläufer *Fregetta tropica* - Brutbiologie, Nahrung, Aktivitätsmuster, Prädation. *Diplomarbeit Friedrich-Schiller-Universität Jena*. 99 pp.
- Hahn, S., H.-U. Peter, P. Quillfeldt and K. Reinhardt** (1998): Population estimates of the birds of Potter Peninsula. *Berichte zur Polarforschung*. **299**:174-181.
- Hahn, S. and P. Quillfeldt** (1998): Different predation pressures on two Antarctic stormpetrel species. *Berichte zur Polarforschung*. **299**:285-289.
- Haig, D.** (1990): Brood Reduction and Optimal Parental Investment When Offspring Differ in Quality. *American Naturalist*. **136**:550-556.
- Hamer, K. C.** (1994): Variability and Stochasticity of Meal Size and Feeding Frequency in the Little Shearwater *Puffinus assimilis*. *Ibis*. **136**:271-278.
- Hamer, K. C. and J. K. Hill** (1993): Variation and Regulation of Meal Size and Feeding Frequency in Corys Shearwater *Calonectris diomedea*. *Journal of Animal Ecology*. **62**:441-450.
- Hamer, K. C. and J. K. Hill** (1994): The Regulation of Food Delivery to Nestling Corys Shearwaters *Calonectris diomedea* - the Roles of Parents and Offspring. *Journal of Avian Biology*. **25**:198-204.
- Hamer, K. C., A. S. Lynnes and J. K. Hill** (1998): Regulation of chick provisioning rate in Manx Shearwaters: experimental evidence and implications for nestling obesity. *Functional Ecology*. **12**:625-630.
- Hamer, K. C., A. S. Lynnes and J. K. Hill** (1999): Parent-offspring interactions in food provisioning of Manx shearwaters: implications for nestling obesity. *Animal Behaviour*. **57**:627-631.
- Hamer, K. C., L. W. Nicholson, J. K. Hill, R. D. Wooller and J. S. Bradley** (1997): Nestling obesity in procellariiform seabirds: temporal and stochastic variation in provisioning and growth of short-tailed shearwaters *Puffinus tenuirostris*. *Oecologia*. **112**:4-11.
- Hamer, K. C., P. Quillfeldt, J. F. Masello and K. L. Fletcher** (2006): Sex differences in provisioning rules: responses of Manx shearwaters to supplementary chick feeding. *Behavioral Ecology*. **17**:132-137.
- Harding, A. M. A., T. I. van Pelt, J. F. Piatt and A. S. Kitaysky** (2002): Reduction of provisioning effort in response to experimental manipulation of chick nutritional status in the horned puffin. *Condor*. **104**:842-847.
-

- Harper, A. B.** (1986): The Evolution of Begging - Sibling Competition and Parent-Offspring Conflict. *American Naturalist*. **128**:99-114.
- Harris, M. P.** (1983): Parent-Young Communication in the Puffin *Fratercula arctica*. *Ibis*. **125**:109-114.
- Harshman, L. G. and A. J. Zera** (2006): The cost of reproduction: the devil in the details. *Trends in Ecology & Evolution*. **22**:80-86.
- Heeb, P., T. Schwander and S. Faoro** (2003): Nestling detectability affects parental feeding preferences in a cavity-nesting bird. *Animal Behaviour*. **66**:637-642.
- Heseker, H. and B. Heseker** (1993): Nährstoffe in Lebensmitteln: die große Energie- und Nährwerttabelle. *Umschau-Verlag*.
- Hipfner, J. M., A. J. Gaston and B. D. Smith** (2006): Regulation of provisioning rate in the Thick-billed Murre (*Uria lomvia*). *Canadian Journal of Zoology-Revue Canadienne de Zoologie*. **84**:931-938.
- Hodum, P. J. and W. W. Weathers** (2003): Energetics of nestling growth and parental effort in Antarctic fulmarine petrels. *Journal of Experimental Biology*. **206**:2125-2133.
- Hornfeldt, B., T. Hipkiss, A. K. Fridolfsson, U. Eklund and H. Ellegren** (2000): Sex ratio and fledging success of supplementary-fed Tengmalm's owl broods. *Molecular Ecology*. **9**:187-192.
- Hudson, P. J.** (1979): Parent-Chick Feeding Relationship of the Puffin, *Fratercula arctica*. *Journal of Animal Ecology*. **48**:889-898.
- Huin, N. and P. A. Prince** (2000): Chick growth in albatrosses: curve fitting with a twist. *Journal of Avian Biology*. **31**:418-425.
- Huin, N., P. A. Prince and D. R. Briggs** (2000): Chick provisioning rates and growth in Black-browed Albatross *Diomedea melanophris* and Grey-headed Albatross *D. chrysostoma* at Bird Island, South Georgia. *Ibis*. **142**:550-565.
- Hussell, D. J. T.** (1988): Supply and Demand in Tree Swallow Broods - a Model of Parent-Offspring Food-Provisioning Interactions in Birds. *American Naturalist*. **131**:175-202.
- Iacovides, S. and R. M. Evans** (1998): Begging as graded signals of need for food in young ring-billed gulls. *Animal Behaviour*. **56**:79-85.
- Johnsen, I., K. E. Erikstad and B. E. Saether** (1994): Regulation of Parental Investment in a Long-Lived Seabird, the Puffin *Fratercula arctica* - an Experiment. *Oikos*. **71**:273-278.
- Johnstone, R. A.** (1995): Honest Advertisement of Multiple Qualities Using Multiple Signals. *Journal of Theoretical Biology*. **177**:87-94.
- Johnstone, R. A.** (1996): Multiple displays in animal communication: 'Backup signals' and 'multiple messages'. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*. **351**:329-338.
- Jurisevic, M. A.** (1999): Structural change of begging vocalisations and vocal repertoires in two hand-raised Australian passerines, the little raven *Corvus mellori* and white-winged chough *Corcorax melanorhamphos*. *Emu*. **99**:1-8.

-
- Kilner, R. and R. A. Johnstone** (1997): Begging the question: Are offspring solicitation behaviours signals of needs. *Trends in Ecology & Evolution*. **12**:11-15.
- Kilner, R. M.** (2002): Sex differences in canary (*Serinus canaria*) provisioning rules. *Behavioral Ecology and Sociobiology*. **52**:400-407.
- Kilner, R. M., D. G. Noble and N. B. Davies** (1999): Signals of need in parent-offspring communication and their exploitation by the common cuckoo. *Nature*. **397**:667-672.
- Krebs, E. A.** (2001): Begging and food distribution in crimson rosella (*Platycercus elegans*) broods: why don't hungry chicks beg more? *Behavioral Ecology and Sociobiology*. **50**:20-30.
- Leech, S. M. and M. L. Leonard** (1997): Begging and the risk of predation in nestling birds. *Behavioral Ecology*. **8**:644-646.
- Leonard, M. L., N. Fernandez and G. Brown** (1997): Parental calls and nestling behavior in tree swallows. *Auk*. **114**:668-672.
- Leonard, M. L. and A. G. Horn** (2001a): Acoustic signalling of hunger and thermal state by nestling tree swallows. *Animal Behaviour*. **61**:87-93.
- Leonard, M. L. and A. G. Horn** (2001b): Begging calls and parental feeding decisions in tree swallows (*Tachycineta bicolor*). *Behavioral Ecology and Sociobiology*. **49**:170-175.
- Lorentsen, S. H.** (1996): Regulation of food provisioning in the Antarctic petrel *Thalassoica antarctica*. *Journal of Animal Ecology*. **65**:381-388.
- Lubjuhn, T. and K. P. Sauer** (1999): Fingerprinting and Profiling in Behavioural Ecology. In: *DNA Profiling and DNA Fingerprinting*. Ed. by J. T. Epplen and T. Lubjuhn. Basel: *Birkhäuser*. pp. 39-52.
- MacGregor, N. A. and A. Cockburn** (2002): Sex differences in parental response to begging nestlings in superb fairy-wrens. *Animal Behaviour*. **63**:923-932.
- Marchant, S. and P. J. Higgins** (1990): Family Hydrobatidae (Oceanitidae) storm-petrels. In: *Handbook of Australian, New Zealand and Antarctic Birds*. Ed. by M. Sharp. Melbourne: *Oxford University Press*. pp. 674-718.
- Martin, T. E.** (1987): Food as a Limit on Breeding Birds - a Life-History Perspective. *Annual Review of Ecology and Systematics*. **18**:453-487.
- Masello, J. F., G. A. Pagnossin, G. E. Palleiro and P. Quillfeldt** (2001): Use of miniature security cameras to record behaviour of burrow-nesting birds. *Die Vogelwarte*. **41**:150-154.
- Miller, D. E. and M. R. Conover** (1983): Chick vocal patterns and non-vocal stimulation as factors instigating parental feeding behaviour in the ring-billed gull *Animal Behaviour*. **31**:145-151.
- Miller, S. A., D. D. Dykes and H. F. Polesky** (1988): A simple salting out procedure for extracting DNA from human nucleated cells. *Nucleic Acids Research*. **16**:1215-1215.
- Mock, D. W., P. L. Schwagmeyer and G. A. Parker** (2005): Male house sparrows deliver more food to experimentally subsidized offspring. *Animal Behaviour*. **70**:225-236.
-

-
- Møller, A. P. and A. Pomiankowski** (1993): Why Have Birds Got Multiple Sexual Ornaments. *Behavioral Ecology and Sociobiology*. **32**:167-176.
- Morton, E. S.** (1977): Occurrence and Significance of Motivation Structural Rules in Some Bird and Mammal Sounds. *American Naturalist*. **111**:855-869.
- Mougeot, F., F. Genevois and V. Bretagnolle** (1998): Predation on burrowing petrels by the Brown Skua (*Catharacta skua lonnbergi*) at Mayes Island, Kerguelen. *Journal of Zoology*. **244**:429-438.
- Mundry, R. and C. Sommer** (2004): Tonal vocalizations in a noisy environment: an approach to their semi-automatic analysis and examples of its application. *Anais Da Academia Brasileira De Ciencias*. **76**:284-288.
- Neuenschwander, S., M. W. G. Brinkhof, M. Kolliker and H. Richner** (2003): Brood size, sibling competition, and the cost of begging in great tits (*Parus major*). *Behavioral Ecology*. **14**:457-462.
- Obst, B. S. and K. A. Nagy** (1993): Stomach oil and the energy budget of Wilson's Storm-Petrel nestlings. *Condor*. **95**:792-805.
- Ottosson, U., J. Backman and H. G. Smith** (1997): Begging affects parental effort in the pied flycatcher, *Ficedula hypoleuca*. *Behavioral Ecology and Sociobiology*. **41**:381-384.
- Oyan, H. S. and T. Anker-Nilssen** (1996): Allocation of growth in food-stressed Atlantic Puffin chicks. *Auk*. **113**:830-841.
- Parker, G. A., N. J. Royle and I. R. Hartley** (2002): Begging scrambles with unequal chicks: interactions between need and competitive ability. *Ecology Letters*. **5**:206-215.
- Peck, D. R. and B. C. Congdon** (2006): Sex-specific chick provisioning and diving behaviour in the wedge-tailed shearwater *Puffinus pacificus*. *Journal of Avian Biology*. **37**:245-251.
- Phillips, R. A. and J. P. Croxall** (2003): Control of provisioning in grey-headed albatrosses (*Thalassarche chrysostoma*): do adults respond to chick condition? *Canadian Journal of Zoology-Revue Canadienne de Zoologie*. **81**:111-116.
- Platzen, D. and R. D. Magrath** (2004): Parental alarm calls suppress nestling vocalization. *Proceedings of the Royal Society of London Series B-Biological Sciences*. **271**:1271-1276.
- Pliquett, R. U., D. Fuhrer, S. Falk, S. Zysset, D. Y. von Cramon and M. Stumvoll** (2006): The effects of insulin on the central nervous system - Focus on appetite regulation. *Hormone and Metabolic Research*. **38**:442-446.
- Price, K.** (1996): Begging as competition for food in Yellow-headed Blackbirds. *Auk*. **113**:963-967.
- Price, K., H. Harvey and R. Ydenberg** (1996): Begging tactics of nestling yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. *Animal Behaviour*. **51**:421-435.

-
- Price, K. and R. Ydenberg** (1995): Begging and Provisioning in Broods of Asynchronously-Hatched Yellow-Headed Blackbird Nestlings. *Behavioral Ecology and Sociobiology*. **37**:201-208.
- Pugesek, B. and K. Diem** (1990): The Relationship between Reproduction and Survival in Known-Aged California Gulls. *Ecology*. **71**:811-817.
- Queller, D. C.** (1997): Why do females care more than males? *Proceedings of the Royal Society of London Series B-Biological Sciences*. **264**:1555-1557.
- Quillfeldt, P.** (2001): Variation in breeding success in Wilson's storm petrels: influence of environmental factors. *Antarctic Science*. **13**:400-409.
- Quillfeldt, P.** (2002a): Begging in the absence of sibling competition in Wilson's storm-petrels, *Oceanites oceanicus*. *Animal Behaviour*. **64**:579-587.
- Quillfeldt, P.** (2002b): Resource partitioning in Wilson's storm-petrels (*Oceanites oceanicus*): adaptations of a small marine bird to breeding in a temporally variable environment. *Dissertation Freie Universität Berlin*. 84 pp.
- Quillfeldt, P.** (2002c): Seasonal and annual variation in the diet of breeding and non-breeding Wilson's storm-petrels on King George Island, South Shetland Islands. *Polar Biology*. **25**:216-221.
- Quillfeldt, P. and J. F. Masello** (2004): Context-dependent honest begging in Cory's shearwaters (*Calonectris diomedea*): influence of food availability. *Acta Ethologica*. **7**:73-80.
- Quillfeldt, P., J. F. Masello and K. C. Hamer** (2004): Sex differences in provisioning rules and honest signalling of need in Manx shearwaters, *Puffinus puffinus*. *Animal Behaviour*. **68**:613-620.
- Quillfeldt, P. and E. Möstl** (2003): Resource allocation in Wilson's storm-petrels *Oceanites oceanicus* determined by measurements of glucocorticoid excretion. *Acta Ethologica*. **5**:115-122.
- Quillfeldt, P. and H.-U. Peter** (2000): Provisioning and growth in chicks of Wilson's storm-petrels (*Oceanites oceanicus*) on King George Island, South Shetland Islands. *Polar Biology*. **23**:817-824.
- Quillfeldt, P., T. Schmoll, H.-U. Peter, J. T. Epplen and T. Lubjuhn** (2001): Genetic Monogamy in Wilson's Storm-Petrel. *Auk*. **118**:242-248.
- Quillfeldt, P., I. J. Strange, G. Segelbacher and J. F. Masello** (2007a): Male and female contributions to provisioning rates of thin-billed prions, *Pachyptila belcheri*, in the South Atlantic. *Journal of Ornithology*. **148**:367-372.
- Quillfeldt, P., I. Trager, K. Griffiths, K. L. Buchanan and J. F. Masello** (2007b): Is sex-specific mass gain in Cory's shearwaters *Calonectris diomedea* related to begging and steroid hormone expression? *Behavioral Ecology and Sociobiology*. **61**:793-800.
- Rahn, H. and A. Ar** (1974): Avian Egg - Incubation-Time and Water-Loss. *Condor*. **76**:147-152.
- Reid, W. V.** (1987): The Cost of Reproduction in the Glaucous-Winged Gull. *Oecologia*. **74**:458-467.
-

- Ricklefs, R. E.** (1987): Response of adult Leach's Storm-Petrels to increased food demand at the nest. *Auk*. **104**:750-756.
- Ricklefs, R. E.** (1992): The roles of parent and chick in determining feeding rates in Leach's Storm-petrel. *Animal Behaviour*. **43**:895-906.
- Ricklefs, R. E., C. H. Day, C. E. Huntington and J. B. Williams** (1985): Variability in feeding rate and meal size of Leach's Stormpetrel at Kent-Island, New Brunswick. *Journal of Animal Ecology*. **54**:883-898.
- Ricklefs, R. E. and W. A. Schew** (1994): Foraging Stochasticity and Lipid-Accumulation by Nestling Petrels. *Functional Ecology*. **8**:159-170.
- Ricklefs, R. E., S. C. White and J. Cullen** (1980): Energetics of Postnatal-Growth in Leachs Storm-Petrel. *Auk*. **97**:566-575.
- Roberts, B.** (1940): The life cycle of Wilson's Petrel *Oceanites oceanicus* (Kuhl). *British Graham Land Expedition Scientific Report*. **1**:141-194.
- Roskaft, E.** (1985): The Effect of Enlarged Brood Size on the Future Reproductive Potential of the Rook. *Journal of Animal Ecology*. **54**:255-260.
- Rowe, C.** (1999): Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour*. **58**:921-931.
- Rowe, C. and J. Skelhorn** (2004): Avian psychology and communication. *Proceedings of the Royal Society of London Series B-Biological Sciences*. **271**:1435-1442.
- Royle, N. J., I. R. Hartley and G. A. Parker** (2002): Begging for control: when are offspring solicitation behaviours honest? *Trends in Ecology & Evolution*. **17**:434-440.
- Ryan, M. J. and E. A. Brenowitz** (1985): The Role of Body Size, Phylogeny, and Ambient Noise in the Evolution of Bird Song. *American Naturalist*. **126**:87-100.
- Ryden, O. and H. Bengtsson** (1980): Differential Begging and Locomotory Behavior by Early and Late Hatched Nestlings Affecting the Distribution of Food in Asynchronously Hatched Broods of Altricial Birds. *Zeitschrift für Tierpsychologie-Journal of Comparative Ethology*. **53**:209-224.
- Sacchi, R., N. Saino and P. Galeotti** (2002): Features of begging calls reveal general condition and need of food of barn swallow (*Hirundo rustica*) nestlings. *Behavioral Ecology*. **13**:268-273.
- Saether, B. E., R. Andersen and H. C. Pedersen** (1993): Regulation of Parental Effort in a Long-Lived Seabird - an Experimental Manipulation of the Cost of Reproduction in the Antarctic Petrel, *Thalassoica antarctica*. *Behavioral Ecology and Sociobiology*. **33**:147-150.
- Saino, N., P. Ninni, M. Incagli, S. Calza, R. Sacchi and A. P. Møller** (2000): Begging and parental care in relation to offspring need and condition in the barn swallow (*Hirundo rustica*). *American Naturalist*. **156**:637-649.
- Schmoll, T.** (2000): Genetisches Paarungssystem und Anpassungswert der Lipidakkumulation im Nestlingsalter bei Buntfußsturmschwalben (*Oceanites oceanicus*) (Kuhl 1820). *Diplomarbeit Friedrich-Schiller-Universität Jena*. 81 pp.

-
- Schwagmeyer, P. L. and D. W. Mock** (2003): How consistently are good parents good parents? Repeatability of parental care in the house sparrow, *Passer domesticus*. *Ethology*. **109**:303-313.
- Siikamäki, P., J. Haimi, M. Hovi and O. Ratti** (1998): Properties of food loads delivered to nestlings in the pied flycatcher: effects of clutch size manipulation, year and sex. *Oecologia*. **115**:579-585.
- Smith, H. G. and R. Montgomerie** (1991): Nestling American Robins Compete with Siblings by Begging. *Behavioral Ecology and Sociobiology*. **29**:307-312.
- Stearns, C.** (1992): The evolution of life histories. New York, *Oxford University Press*.
- Stonehouse, B.** (1989): Polar Ecology. New York, *Blackie/Chapman and Hall*.
- Takahashi, A., M. Kuroki, Y. Niizuma and Y. Watanuki** (1999a): Parental food provisioning is unrelated to manipulated offspring food demand in a nocturnal single-provisioning alcid, the Rhinoceros Auklet. *Journal of Avian Biology*. **30**:486-490.
- Takahashi, A., Y. Niizuma and Y. Watanuki** (1999b): Regulation of food provisioning and parental body condition in Leach's storm-petrels, *Oceanodroma leucorhoa*: Experimental manipulation of offspring food demand. *Ecological Research*. **14**:155-164.
- Taylor, J. R. E. and M. Konarzewski** (1992): Budget of Elements in Little Auk (*Alle alle*) Chicks. *Functional Ecology*. **6**:137-144.
- Thomas, D. W., C. Bosque and A. Arends** (1993): Development of Thermoregulation and the Energetics of Nestling Oilbirds (*Steatornis caripensis*). *Physiological Zoology*. **66**:322-348.
- Trager, I., J. F. Masello, R. Mundry and P. Quillfeldt** (2006): Do acoustic parameters of begging calls of Cory's Shearwaters *Calonectris diomedea* reflect chick body condition? *Waterbirds*. **29**:315-320.
- Trivers, R. L.** (1974): Parent-offspring conflict. *American Zoologist*. **14**:249-264.
- Villaseñor, E. and H. Drummond** (2007): Honest begging in the blue-footed booby: signaling food deprivation and body condition. *Behavioral Ecology and Sociobiology*. **61**:1133-1142.
- Warham, J.** (1977): The incidence, functions and ecological significance of Petrel stomach oils. *Proceedings of the New Zealand Ecological Society*. **24**:84-93.
- Warham, J.** (1990): The Petrels - their Ecology and Breeding Systems. London, *Academic Press*.
- Warham, J.** (1996): The Behaviour, Population Biology and Physiology of the Petrels. London, *Academic Press*.
- Warham, J., B. R. Keeley and G. J. Wilson** (1977): Breeding of Mottled Petrel. *Auk*. **94**:1-17.
- Warham, J., R. Watts and R. J. Dainty** (1976): The composition, energy content and function of the stomach oils of Petrels (Order Procellariiformes). *Journal of Experimental Marine Biology and Ecology*. **23**:1-13.
-

-
- Wasilewski, A.** (1986): Ecological aspects of the breeding cycle in the Wilson's storm petrel, *Oceanites oceanicus* (Kuhl), at King George Island (South Shetland Islands, Antarctica). *Polish Polar Research*. **7**:173-216.
- Weimerskirch, H., A. Ancel, M. Caloin, A. Zahariev, J. Spagiari, M. Kersten and O. Chastel** (2003): Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick. *Journal of Animal Ecology*. **72**:500-508.
- Weimerskirch, H., O. Chastel and L. Ackermann** (1995): Adjustment of Parental Effort to Manipulated Foraging Ability in a Pelagic Seabird, the Thin-Billed Prion *Pachyptila belcheri*. *Behavioral Ecology and Sociobiology*. **36**:11-16.
- Weimerskirch, H., Y. Cherel, F. Cuenot-Chaillet and V. Ridoux** (1997a): Alternative foraging strategies and resource allocation by male and female Wandering Albatrosses. *Ecology*. **78**:2051-2063.
- Weimerskirch, H. and P. Lys** (2000): Seasonal changes in the provisioning behaviour and mass of male and female wandering albatrosses in relation to the growth of their chick. *Polar Biology*. **23**:733-744.
- Weimerskirch, H., T. Mougey and X. Hindermeier** (1997b): Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behavioral Ecology*. **8**:635-643.
- Weimerskirch, H., P. A. Prince and L. Zimmermann** (2000): Chick provisioning by the Yellow-nosed Albatross *Diomedea chlororhynchos*: response of foraging effort to experimentally increased costs and demands. *Ibis*. **142**:103-110.
- Wells, J. C. K.** (2003): Parent-offspring conflict theory, signaling of need, and weight gain in early life. *Quarterly Review of Biology*. **78**:169-202.
- Wernham, C. V. and D. M. Bryant** (1998): An experimental study of reduced parental effort and future reproductive success in the puffin, *Fratercula arctica*. *Journal of Animal Ecology*. **67**:25-40.
- Williams, G. C.** (1966): Natural Selection Costs of Reproduction and a Refinement of Lack's Principle. *American Naturalist*. **100**:687-690.
- Wright, J., C. Hinde, I. Fazey and C. Both** (2002): Begging signals more than just short-term need: cryptic effects of brood size in the pied flycatcher (*Ficedula hypoleuca*). *Behavioral Ecology and Sociobiology*. **52**:74-83.
- Wunderle, S., H. Saurer and H. Goßmann** (1998): Meteorological Conditions and Snow Cover Dynamics on the Potter Peninsula, King George Island, Antarctica. *Reports on Polar Research*. **299**:15-27.
- Ydenberg, R.** (1994): The behavioral ecology of provisioning in birds. *Ecoscience*. **1**:1-14.

8. Appendix

Appendix A Influence of experimental supplementation on the classic call parameters, the acoustic call features and the PCA factors. To control for individual effects *nest* was included as fixed factor in the GLM. Significant *P* – values are marked bold.

Source	Both seasons			2005			2006		
	d.f.	F	P	d.f.	F	P	d.f.	F	P
Number of long calls									
Treatment	1	0.001	0.973	1	1.845	0.186	1	4.856	0.038
Nest	27	3.794	< 0.001	16	3.676	0.002	10	5.351	0.001
Total	77			43			34		
Call rate									
Treatment	1	3.629	0.063	1	6.788	0.015	1	0.027	0.872
Nest	27	5.724	< 0.001	16	4.877	< 0.001	10	9.632	< 0.001
total	78			43			35		
Maximum call rate									
Treatment	1	0.161	0.690	1	0.032	0.860	1	0.789	0.384
Nest	27	5.946	< 0.001	16	4.986	< 0.001	10	8.120	< 0.001
total	78			43			35		
Duration of begging session									
Treatment	1	3.420	0.071	1	0.548	0.466	1	5.361	0.030
Nest	27	2.732	0.001	16	2.266	0.032	10	3.922	0.004
total	77			43			34		
Duration of single long call									
Treatment	1	0.211	0.849	1	8.318	0.011	1	1.604	0.218
Nest	27	4.373	< 0.001	16	2.645	0.030	10	5.102	0.001
total	69			34			35		
FMax									
Treatment	1	7.861	0.008	1	5.518	0.032	1	2.555	0.124
Nest	27	17.813	< 0.001	16	4.589	0.002	10	9.998	< 0.001
total	69			34			35		
FMean									
Treatment	1	7.806	0.008	1	10.272	0.006	1	0.095	0.761
Nest	27	16.559	< 0.001	16	4.207	0.003	10	25.193	< 0.001
total	69			34			35		
LocFMax									
Treatment	1	0.005	0.941	1	0.199	0.662	1	0.063	9.805
Nest	27	1.101	0.384	16	1.654	0.162	10	0.347	0.957
total	69			34			35		
LFMaxAbs									
Treatment	1	0.117	0.734	1	1.702	0.210	1	0.143	0.709
Nest	27	1.598	0.087	16	1.545	0.197	10	1.754	0.128
total	69			34			35		

Appendix A (continued) Influence of experimental supplementation on the classic call parameters, the acoustic call features and the PCA factors. To control for individual effects *nest* was included as fixed factor in the GLM. Significant *P*-values are marked bold.

Source	Both seasons			2005			2006		
	d.f.	F	P	d.f.	F	P	d.f.	F	P
SISStMax									
Treatment	1	0.219	0.642	1	2.910	0.107	1	0.806	0.378
Nest	27	1.536	0.107	16	1.382	0.263	10	0.942	0.515
total	69			34			35		
SIMaxEnd									
Treatment	1	3.958	0.054	1	6.004	0.026	1	0.044	0.836
Nest	27	6.341	< 0.001	16	4.870	0.001	10	0.614	0.787
total	69			34			35		
LMaxAmp									
Treatment	1	1.156	0.289	1	2.054	0.171	1	0.000	0.994
Nest	27	2.652	0.003	16	1.654	0.162	10	2.759	0.021
total	69			34			35		
LMA_Abs									
Treatment	1	1.364	0.250	1	6.118	0.025	1	1.073	0.311
Nest	27	2.363	0.007	16	2.300	0.053	10	3.666	0.005
total	69			34			35		
PeakFTot									
Treatment	1	7.438	0.009	1	11.524	0.004	1	0.118	0.735
Nest	27	11.726	< 0.001	16	3.613	0.007	10	24.412	< 0.001
total	69			34			35		
BroadTot									
Treatment	1	0.662	0.421	1	0.000	0.986	1	1.823	0.190
Nest	27	2.874	0.001	16	1.557	0.193	10	2.408	0.039
total	69			34			35		
PCA factor 1									
Treatment	1	6.661	0.014	1	9.252	0.008	1	0.030	0.865
Nest	27	11.361	< 0.001	16	3.422	0.009	10	10.921	< 0.001
total	69			34			35		
PCA factor 2									
Treatment	1	0.421	0.520	1	3.897	0.066	1	1.258	0.274
Nest	27	2.294	0.008	16	2.195	0.063	10	0.856	0.584
Total	69			34			35		
PCA factor 3									
Treatment	1	0.008	0.928	1	0.191	0.668	1	0.040	0.844
Nest	27	1.071	0.415	16	1.494	0.215	10	0.835	0.601
total	69			34			35		
PCA factor 4									
Treatment	1	1.073	0.306	1	3.339	0.086	1	0.588	0.451
Nest	27	1.973	0.025	16	1.475	0.223	10	3.772	0.004
total	69			34			35		

Appendix B

List of abbreviations and terms

<i>A</i>	Growth asymptote
ANOVA	Analysis of Variance
BroadTot	Frequency breadth of the element
chick-night	One night per individual chick
Duration	Duration of long begging call
FFT-length	Fast Fourier transform length; algorithm
FMax	Maximum frequency of the call element
FMean	Mean frequency of the call element
GLM	General Linear Models
k_t	Tarsus growth rate
k_{tf}	Growth rate of eighth primary
k_w	Wing growth rate
LFMaxAbs	Absolute location of FMax from beginning of the element
LMA_Abs	Absolute location of maximum amplitude from beginning of the element
LMaxAmp	Relative location of maximum amplitude normalised to element's duration
LocFMax	Relative location of FMax normalised to element's duration
PCA	Principal Component Analysis
PeakFtot	Loudest frequency
SLA battery	Sealed lead acid battery
SIMaxEnd	Difference in frequency from FMax to element's end divided by the duration LFMaxAbs to the end
SIStMax	Difference in frequency from start to FMax divided by LFMaxAbs

9. Acknowledgements

Prof. Stefan Halle and Dr. Hans-Ulrich Peter supervised this diploma thesis. I want to thank them for providing me this unique opportunity to work in this stunning part of the world. Special thanks to Dr. Hans-Ulrich Peter who organised permissions, logistic and financial support enabling me to concentrate on the work with the storm-petrels.

Many thanks to all ‘Sturmies’, i.e. Christina Braun, Anja Gladbach and Dr. Petra Quillfeldt, who had the idea to conduct a feeding experiment in combination with the infrared recording of nightly feedings, introduced me to the storm-petrels and gave useful advises and comments on the handling of the birds, as well as helpful comments on the manuscript.

For fruitful discussions, interesting hints, tips and jokes (although mainly at my expenses) during Mate-breaks and beyond I want to thank all members of the Polar & Bird Ecology Group. In particular:

Dr. Simone Pfeiffer and Christina Braun, who critically read the first version of this thesis. Furthermore, they provided (amongst others) moral support whenever needed and are jointly responsible that I enjoyed the time being part of this working group.

Matthias Kopp, who spent two field seasons with me in Jubany, cooperatively lugging the heavy batteries with me to the film nests or burning the midnight oil to join me mistnetting storm-petrels (although falling asleep occasionally) after a long and exhausting day of his own fieldwork. Thanks for being a friend far away from home.

Markus Ritz, who helped me (more readily than expected) with all problems and questions arising in the lab or with the statistics.

Financial support was partly provided by the German Research Foundation (DFG PE 454) and the Federal Ministry of Education and Research (DLR). Logistic support came from the Alfred Wegener Institute for Polar and Marine Research, Fuerza Aérea de Chile, Fuerza Aérea Uruguay and Hapag-Lloyd Cruises.

Last but not least I want to thank my parents for supporting me in every respect and for always putting up with my caprices.

10. Selbständigkeitserklärung

Hiermit versichere ich, dass ich die vorliegende Diplomarbeit

Nestling begging strategies in Wilson's storm-petrels (Oceanites oceanicus)

–

Insights from a supplementary feeding experiment

selbständig und nur unter Verwendung der angegebenen Hilfsmittel und Literatur angefertigt habe.

Jena, am 18. September 2007

.....

Anja Nordt